# The ecology of the short fin eel *Anguilla australis schmidtii* in Lake Ellesmere, Canterbury

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# INTRODUCTION

Eels of the genus *Anguilla* are an important food fish in many parts of the world. Principally because of this gastronomic interest, there has been much research into various aspects of their biology. Most of this research has been on the juvenile stage, the yellow (or feeding) eel, which feeds and grows in freshwater before returning to the sea as it nears sexual maturity.

Eels are an important food fish in European diets, so it is not surprising that most published work comes from that area. Frost (1945, 1946) studied feeding and growth of the European eel, *A. anguilla* Linnaeus in the English Lake District. Since then, there have been comprehensive studies on age, growth and feeding by Sinha and Jones (1967a, 1967b) on eels from Welsh rivers and by Moriarty (1972, 1973) on eels from Irish lakes. There have been extensive reviews of biological information on the eel by Deelder (1971) and Tesch (1973).

North American research has been less comprehensive and most studies have concentrated on either age and growth, or the feeding of *A. rostrata* Le Sueur. The most important age and growth studies have been by Gray and Andrews (1971) and Liew (1974). Godfrey (1957) and Wenner (1972) carried out feeding studies.

In New Zealand there are two species of freshwater eel, the short fin, *A. a. schmidtii* Phillipps, and the long fin, *A. dieffenbachi* Gray. While both species are found throughout most freshwaters, in general terms the smaller *A. a. schmidtii* tends to be coastal and the larger *A. dieffenbachi* more inland. Skr zynski (1974) reviewed the biology of both species of eel. Both species were top order predators until the introduction (towards the end of the 19th century) of rainbow trout, *Salmo gairdneri* Richardson and brown trout, *Salmo trutta* Linnaeus. Concern over predation by eels on trout and the possible effects on interspecific competition for food, provided the necessary stimulus for early work by Cairns (1941, 1942) on the general biology of both species. Other comprehensive studies have been carried out by Burnet (1952, 1969a, 1969b).

Additional feeding studies have been by Woods (1964), Hopkins (1965, 1971), Crossland (1972) and Cadwallader (1975).

With the exception of the work of Crossland, the information presented on feeding in these studies was incidental to the main aims of the research.

In Lake Ellesmere, Canterbury, Hobbs (1947) studied migrant eels of both species, with a view to determining population numbers so that a fish oil extraction industry could be established. Lake Ellesmere has been subjected to increasing fishing pressure since, and the fishery has grown so that the lake eels now provide the basis of the most important eel fishery in New Zealand. Because there have been no studies on the eel population since that of Hobbs, and as there is no published work on the feeding ecology of eels in lakes, a comprehensive study programme on *A. a. schmidtii* was initiated in Lake Ellesmere. The long fin, *A. dieffenbachi* did not occur commonly enough to enable it to be studied.

The objectives of this study were to determine the feeding periodicity and the type and number of each prey species in the diet of *A. a. schmidtii*, evaluated in calorific terms. Laboratory experiments on gastric evacuation were planned, to enable a daily ration to be calculated from the feeding data. It was also hoped to back calculate growth rates from otoliths to give information on the effect of fishing pressures on the population, and allow comparisons with the growth rates of other *Anguilla* species. This growth data, together with results from laboratory assimilation experiments, would enable a daily energy budget for the eel to be derived.

# CHAPTER ONE. FOOD AND FEEDING PERIODICITY

## INTRODUCTION

Knowledge of the food of a fish species is fundamental to any study involving feeding behaviour, growth rates or energy budgets. Studies on the food of the eel have been mainly on the European eel, *Anguilla anguilla*, probably because it is an important food fish. Hartley (1940), Frost (1946), Draganik (1962), Thomas (1962), Cragg-Hine (1964), Rogers (1964), Sinha and Jones (1967b), Moriarty (1972, 1973), Shafi and Maitland (1972), Biro (1974) and Moore and Moore (1976) have all worked on some aspect of the feeding biology of *A. anguilla*. The results obtained depended upon the size of the eels examined and the habitat in which they were caught. In general these studies found that eels will feed upon most organisms of suitable size that are available in their environment. Many of these authors report that feeding is seasonal with the lowest intensity in winter.

Perhaps because it is not considered an important food fish, the American eel, *Anguilla rostrata* has not been so comprehensively investigated. Godfrey (1957), Ogden (1970), Wenner (1972), and Wenner and Musick (1975) have all studied aspects of feeding in this eel and arrive at conclusions similar to those of the European workers.

Although there is no information on the food habits of wild Japanese eel, *Anguilla japonica* Temminck and Schlegel, there is comprehensive data on the feeding of cultured eels.

The New Zealand eels, *Anguilla dieffenbachi* and *Anguilla australis schmidtii* have been studied with respect to their feeding biology by Cairns (1942), Burnet (1952, 1969a) and Hopkins (1965, 1970). Cairns examined guts from 9 643 eel from a wide variety of habitats but noted only the number of each prey species present. Burnet and Hopkins both studied the feeding habits of eels in streams, so apart from the investigation by Cairns, there has been no work published on eel feeding in lakes.

## LOCALITY

The study area was the southern end of Lake Ellesmere (45°45'S, 172°30'E), near Taumutu. Lake Ellesmere is a large coastal lake on the east of the South Island and 45 km south of Christchurch. The lake is separated from the sea only by the Kaitorete spit. Periodic openings through the spit (three to four times per year), waves washing over and seepage of seawater cause the lake to be slightly saline. Chloride levels quoted by Hughes *et al.* (1974) range from 1 540 g per $m^3$ to 11 300 g per $m^3$. The mean depth of the lake is 2.1 m at mean sea level (m.s.l.). When opened to the sea the level equilibrates at approximately 0.45 m above m.s.l. but if the spit has been closed for some time, the level may reach 1.06 m above m.s.l. and wind action may raise the level on the leeward shore by up to 0.68 m. The surface area of the lake ranges from 15 790 ha to 20 250 ha. The few chemical analyses of lake water and available information on the algae indicate that the lake is mesotrophic to eutrophic (Hughes *et al.* 1974).

The study area was on the north bank of the Taumutu arm of the lake (Fig. 1), approximately midway between the lake proper and a small stream at the head of the inlet. This area was selected for six reasons:

a) There were no apparent biological reasons for preferring any other area for sampling.
b) It was easily accessible.
c) Equipment could be left on private land.
d) It was relatively sheltered.
e) The water was shallow enough (<2 m) to allow setting of nets without a boat.
f) Accommodation was often available.

In the study area the bottom substrate was mainly mud with scattered areas of shingle and occasional small stones up to 10 cm in diameter. The small stream at the western end produced a slight salinity gradient, with salinity increasing up the arm towards the lake proper (Ryan, 1972).

Lake temperatures near Taumutu, recorded monthly from July 1973 to June 1974 by the North Canterbury Catchment Board, ranged from 6°C in June to 19°C in March (pers. comm.).

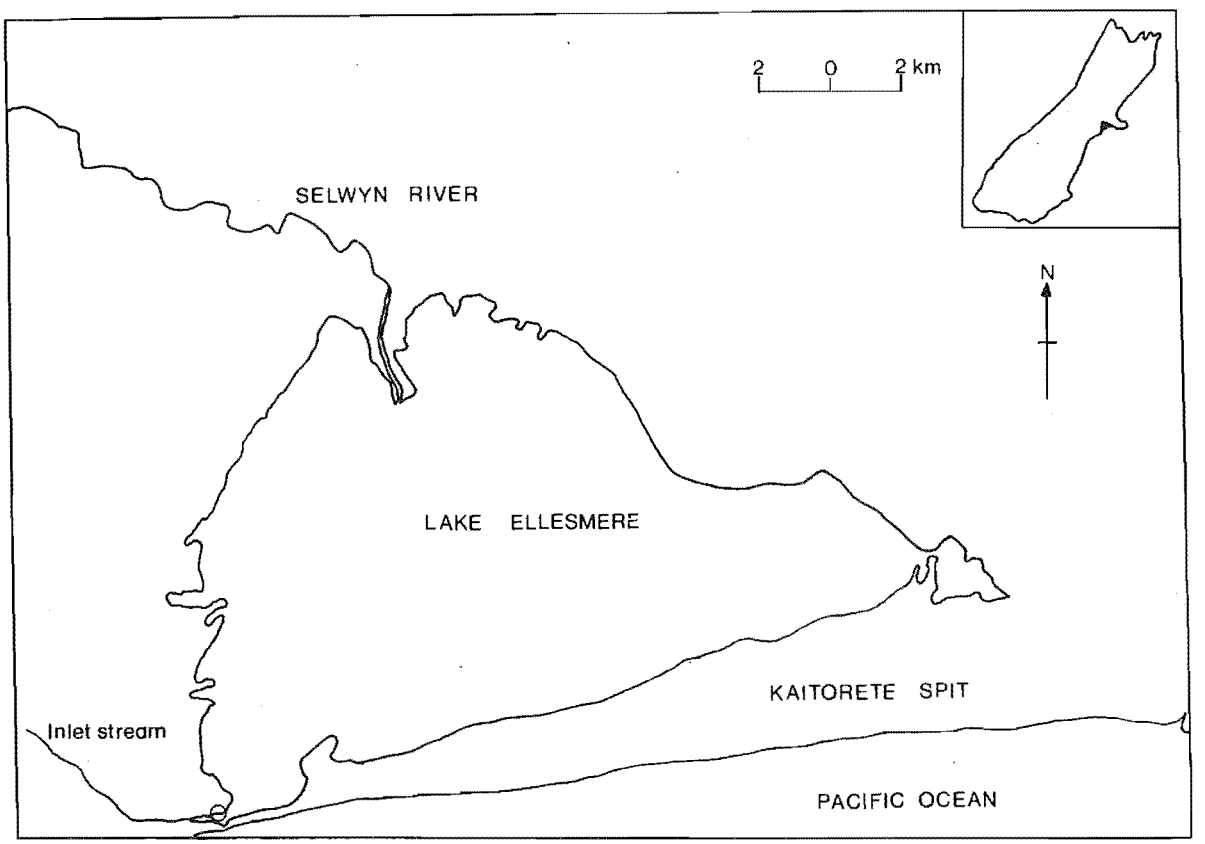


Fig. 1. Lake Ellesmere (approximate position of the sample area at Taumutu is given by o).

Readings taken in the study area during sampling trips ranged from 5°C in June and July 1975 to 21°C in March 1974. A maximum/minimum thermometer left on the bottom during 1975, and read on each sampling trip, recorded a minimum temperature of 4°C in June (when the arm was iced over) and a maximum of 21°C in March.

There was little aquatic vegetation at the sampling site but occasional clumps of *Potamogeton pectinatus*, *Ruppia megacarpa* and *Elodea canadensis* were encountered. The rush *Juncus maritimus* was common near the water's edge. Terrestrial plants were frequently inundated because of fluctuations in lake level. The general appearance of the sample site is shown in Plate 1.

Invertebrates collected are recorded in Table 9 and an incomplete list for the lake is quoted by Hughes *et al.* (1974). The most abundant invertebrates were the crustaceans *Tenagomysis chiltoni*, *Paracorophium excavatum*, *Paracalliope fluviatilis* and *Austridotea annectens*, the mollusc *Potamopyrgus antipodarum*, larvae of the dipteran *Chironomus zealandicus*, the hemipterans *Sigara arguta* and *Diaprepocoris zealandiae* and damselfly larvae, *Xanthocnemis zealandica* and *Austrolestes colensonis*.

The fish present have been listed by Ryan (1974). The most common fish found are the bully *Gobiomorphus cotidianus*, the inanga *Galaxias attenuatus*, the smelt *Retropinna retropinna* and the subject of this study, the shortfinned eel *Anguilla australis schmidtii*.

Plate 1. View of sample area looking west along the arm. The poles anchor commercial eel fyke nets.

## METHODS

### Sampling

Sampling was undertaken at approximately monthly intervals, from January 1974 to April 1976, using two Danish fyke nets. Details of dates of sampling trips, number of nets used, and numbers of eels caught are given in Table 1. Sampling generally began at 1200 h and nets were examined at three-hourly intervals until 1200 h the following day. When weather conditions were poor, or in winter when low catch rates did not justify three-hourly examination, nets were set at night and harvested at first light the following morning.

The nets had a hoop diameter of 0.65 m, a funnel opening of 0.25 m, and a leader length of 2 m and were covered with 25.4 mm (1") green nylon mesh. The nets were set at right angles to the shoreline in one metre of water, which was usually about 5 m from the lake shore. Additional fyke nets were occasionally borrowed from commercial eel fishermen to try to increase catch rates during winter. Moriarty (1972) has shown considerable differences in catch rates depending on such factors as leader length, colour of net, hoop size and mesh size. The effect of these factors on catch size in Lake Ellesmere was not known. However, eels caught in borrowed nets (which were different from the two Danish fykes used regularly) were used in calculations of catch rates per net night. This seems justifiable in view of the fact that the nets were only borrowed at times when eels were difficult to catch and did not markedly affect the total number of fish caught.

Difficulties were occasionally met with during north-westerly winds which banked water to a height which made it difficult to empty nets safely in chest waders. Rough weather conditions upset three sampling trips by dislodging the nets. The most unusual problem faced was during the migration period of sexually maturing adult eels (March and April) when, in one three-hour period, 600 (non-feeding) migrants were caught, thus effectively clogging the net and preventing capture of non-migrants.

Fyke nets are size-selective, as small eels can force their way through the mesh. Other methods of catching eels

Table 1. Dates of sampling trips, number of eels captured, and the number of nets used.

| Date | Number of eels captured | Number of nets used |
|---|---|---|
| 17 January 1974 | 28 | 2 |
| 27 February 1974 | 4 | 2 |
| 13 March 1974 | 3 | 2 |
| 5 April 1974 | 9 | 2 |
| 27 April 1974 | 13 | 2 |
| 2 May 1974 | 5 | 2 |
| 5 June 1974 | 0 | 2 |
| 18 June 1974 | 0 | 2 |
| 23 July 1974 | 5 | 2 |
| 19 September 1974 | 15 | 1 |
| 4 October 1974 | 0 | 2 |
| 18 October 1974 | 31 | 2 |
| 6 November 1974 | 47 | 2 |
| 22 December 1974 | 6 | 2 |
| 18 January 1975 | 28 | 2 |
| 19 February 1975 | 30 | 2 |
| 5 April 1975 | 49 | 2 |
| 30 April 1975 | 12 | 6 |
| 17 July 1975 | 5 | 6 |
| 6 August 1975 | 0 | 4 |
| 25 August 1975 | 0 | 2 |
| 26 August 1975 | 7 | 4 |
| 27 August 1975 | 4 | 6 |
| 28 August 1975 | 1 | 6 |
| 23 September 1975 | 4 | 4 |
| 14 October 1975 | 99 | 1 |
| 1 December 1975 | 37 | 1 |
| 25 February 1976 | 2 | 2 |
| 29 February 1976 | 5 | 2 |
| 7 April 1976 | 38 | 2 |

were considered but were dismissed because of practical difficulties. Electric fishing could not be used as a recent fatality caused a ban to be placed on the use of electric fishing machines throughout New Zealand. Also, brackish water is difficult or impossible to electric fish because of its high conductance. It is likely therefore that electric fishing would not have been possible even in the absence of a ban. Because alternative methods were not feasible it was decided to work only on those size classes of eel which the net could effectively catch. Moriarty (1972) showed that eels as small as 28 cm long could be caught with 20 and 22 mm mesh nets. In the present study eels as small as 23 cm were captured.

The removal of eels during a sampling period might reduce the number of eels available for capture in subsequent time intervals if the population from which the samples were drawn was small. This possibility was checked on 1 December 1975, by using one net for the collection of fish for stomach samples and the other net, 40 m away, for capture and release. 27 eels caught in the second net were tagged sub-epidermally with a UV light fluorescent dye (see Ryan, 1975) and released. All 40 eels caught in the nets during the sample period were examined with a portable UV light source but no tagged eels were recaptured. It is possible that handling the tagged eels may have made them net-shy but catch rates did not drop during the evening, so that it seems unlikely that the eel density was being significantly reduced by the sampling programme. Further support for this assumption comes from the activities of eel fishermen, who sometimes leave nets in one position for the whole season without experiencing any significant reduction in capture rates.

Field treatment of eels

After collection, eels were killed with benzocaine and total length (from the anterior extremity to the end of the tail fin) was measured to the nearest 1 mm on a V-shaped measuring board. The abdomen was opened and the stomach injected with 10% formalin solution to prevent further digestion of contents. The stomach was removed and preserved in 10% formalin for future analysis, and the intestine was removed and discarded. Each eel was then weighed to the nearest gram on

an Ohaus beam balance. Using only gutted eels reduced the variability in eel weight due to different degrees of gut fullness. Condition factor was calculated, using the relationship

$$K = CW/\ell^b$$

where C is a constant, W is fish weight in g, $\ell$ is fish length in mm and b is either 3 or a true value calculated from a log weight/log length regression.

Otoliths were obtained by cutting with a knife at right angles to the vertebral column just posterior to the cranium to two thirds the depth of the animal. A further cut along the midline of the fish through the cranium and roof of the mouth to the lower jaw bifurcated the skull. Sagittal otoliths were then removed, cleaned and placed in dry vials for later use in age determination. This method, although similar to that described by Moriarty (1975), was slightly improved as the heavy duty blade of the knife was better at splitting large crania than the scissors used by Moriarty. Whenever possible eels were sexed in the field using the criteria given by Todd (1974), although only females greater than 50 cm total length could be identified positively so that, in practice, catch information consisted primarily of female and undifferentiated fish.

Stomach analysis

The stomachs of 487 fish were analysed during the study. Stomachs were opened in the laboratory, and their contents placed in petri dishes and sorted. Where possible each food organism was identified to species.

Early analysis indicated that *Potamopyrgus antipodarum*, *Austridotea annectens*, *Tenagomysis chiltoni*, *Paracalliope fluviatilis*, *Chironomus zealandicus* larvae, *Gobiomorphus cotidianus*, *Galaxias maculatus* and *Retropinna retropinna* together made up at least 90% by volume of the diet. The pre-ingested weight of each of these organisms was required to calculate percentage digestion and to determine the pre-ingested calorific value. To determine pre-ingested weight it was necessary, where prey animals did not remain intact, to identify and measure some digestion-resistant hard part and relate the length obtained to the total length and dry weight of prey animals of the same species collected in the field. Where

possible total length of prey species or, in fragmented specimens, some standardised hard part was measured by projecting their image onto paper using a camera lucida attached to an Olympus binocular microscope. Lengths were traced and this line converted to millimetres using a scale calibrated with a stage micrometer. The scale used depended on the degree of magnification required, which varied from x 6.3 to x 40. Total length of *P. antipodarum* with broken shells was not obtainable so the diameter of the shell aperture was used as this strengthened part of the shell was the last to be broken in the stomachs. (These measurements were at x 10 magnification to the nearest 0.1 mm). The exoskeletons of *A. annectens* were relatively resistant to digestion and in very few cases was it not possible to measure total length. In well digested specimens the telson remained intact for the greatest length of time, so telson length was related to total length by measuring each to the nearest 0.1 mm using x 6.3 magnification. Data from 59 animals was used to fit a regression line relating telson length to total length. For *T. chiltoni* carapace length was adopted as the standard measurement as it was large relative to the total length of the animal, digestion resistant and easily identifiable. Each carapace was measured to the nearest 0.05 mm. Head capsule lengths of *C. zealandicus* were measured to the nearest 0.01 mm at x 40 magnification. Lengths, rather than widths, were chosen as head capsules were often crushed and then appeared wider than normal capsules. No linear measurements were made of *Paracalliope fluviatilis* as there were no large, relatively identifiable hard parts and total length varied with the degree of digestion.

The total length of *G. cotidianus* was measured to the nearest 1.0 mm using a pair of Mitutoyo calipers. If only the cranium and vertebral column remained intact their total length was assumed to be the same length as the standard length of the living animal. If only sections of the vertebral column remained, the fish was not identifiable but was recorded as an average sized *G. cotidianus*. The same method was used for *R. retropinna* and *G. maculatus*.

All prey organisms from each stomach were placed in aluminium foil bottle caps of known weight, one species per cap, and dried at 70°C to constant weight. The mean digested dry weight

of each organism was then calculated for later comparison with its predicted pre-ingested weight.

Length, dry weight and calorific value determination of prey species

Collections of *A. annectens*, *T. chiltoni* and *G. cotidianus* were made in May, August and November 1975 and January 1976 to determine lengths, dry weights and calorific values. Animals were collected from the arm of the lake or the inlet stream at the head of the arm. It was intended also to collect *P. antipodarum* seasonally, but catastrophic flooding in the inlet stream decimated the population in May and recolonisation was slow so collections were made in August and November 1975 and January 1976 only.

*P. antipodarum* shell aperture diameter and total length were measured using a camera lucida as previously described and each shell was assigned to a length class. The size class depended to some extent on availability but was generally <3.0, 3.1 to 4.0, 4.1 to 4.5, 4.6 to 5.0 and >5.0 mm. Mean weights of each size class were determined by drying to constant weight at 70°C and weighing on a Mettler balance to the nearest 0.1 mg. Shell aperture diameter/dry weight and total length/dry weight regression lines were fitted by computer. All size classes were homogenised in a Waring commercial blender and compacted into pellets weighing about 0.1 g. As water had to be added to bind the pellets each was dried to a constant weight at 70°C and weighed to the nearest 0.1 mg. This general procedure was followed for all calorific work and is similar to that outlined by Prus (1975). Calorific values were determined with a Parr oxygen bomb calorimeter, which was first standardised using benzoic acid pellets of known calorific value. Once calorific values for each size class had been obtained, they were converted to joules and tables for energy value/length for each season compiled. Carapace length was used to determine length classes of *T. chiltoni* which were usually <3.00, 3.05 to 3.50, 3.55 to 4.00, 4.05 to 4.50 and >4.55 mm. *A. annectens* was divided into 1 mm length classes, but had marked seasonal differences in length and some size classes were not always available. Length/dry weight regressions were computer fitted for the four different months for *A. annectens* and *T. chiltoni*.

Calorific values for each size class of these two species were determined and tables for energy value/length for each season compiled. Although no linear measurements were made of *P. fluviatilis* (for reasons already described), summer (January) calorific values of the population as a whole were determined. In eels which had eaten *P. fluviatilis*, it was assumed that the average degree of digestion of the organisms for which pre-ingested weights were known (e.g. the other peracarid, *A. annectens*) would serve as an indicator of the degree of digestion of the amphipods. This assumption is very similar to that made by Darnell and Meierotto (1962) in their studies on natural fish populations. *G. cotidianus* were killed with benzocaine and, after being rolled in a towel to remove excess water, were weighed to the nearest 1 mg on a Mettler top pan balance. The standard length was measured to 0.1 mm using Mitutoyo calipers and each fish then dried to a constant weight at 70°C, re-weighed and length/dry weight regression lines for each season computer fitted. All size classes were then homogenised and bomb calorimeter pellets manufactured. After calorimetry, tables of calorific values for each season were calculated.

*G. maculatus* were collected in February 1978 for length/dry weight determinations. Unfortunately, live *R. retropinna* could not be collected in February 1978, so formalin preserved fish caught in January 1977 were used to determine length/dry weight relationships and calorific value.

It was not possible to collect *C. zealandicus* larvae from the study area in adequate numbers. Larvae were therefore obtained from the oxidation ponds of the Christchurch Drainage Board at Bromley, and others were collected at Lake Grasmere, an inland freshwater lake. Head capsule lengths were used to assign larvae into instars, after determining the relationship between head width (which is normally used to assign larvae into instars (Robb, 1966) and length. In practice only 4th instar larvae were used as the first three instars were not abundant enough to make pellets for satisfactory calorimetry. Comparison of head capsule lengths with those lengths obtained from ingested larvae showed that the vast majority of *C. zealandicus* larvae eaten by the eels were fourth instar. All larvae collected were dried to constant dry weight at 70°C and a mean

dry weight for the instar determined. Calorific values were obtained by pelleting the larvae and carrying out bomb calorimetry.

Whenever frequency of occurrence of a prey organism in the eel stomachs was too low to warrant regular collection of the species for calorimetry, values for the closest related species were obtained from Cummins and Wuycheck (1971).

Analysis of data

To enable maximum utilisation of available data it was considered that as many different measures as possible of feeding success should be utilised. This approach also enabled comparison to be made between the different methods. Methods chosen were:

a) Visual estimate of fullness. A visual estimate of the stomach fullness was made using a scale devised by Ball (1961) and subsequently modified by Hunt and Jones (1972). This index provides a way of examining seasonal changes in the quantities of food eaten. No information on the composition of the diet is given.

| Visual estimate of stomach fullness | Points |
|---|---|
| Distended | 10 |
| Full | 8 |
| 3/4-full | 6 |
| 1/2-full | 4 |
| 1/4-full | 2 |
| Trace | 1 |
| Empty | 0 |

b) Frequency of occurrence. The number of stomachs in which each food species occurred was recorded and expressed as a percentage of the total number of stomachs. This method indicates composition of the diet but does not give quantitative estimates of the amounts of different foods present. It tends to overemphasise the importance of digestion resistant items (Windell, 1971).

c) Numerical method. The numbers of individuals of each food species expressed as a percentage of the total number of all organisms present in the stomach. The method overempha-

sises the importance of small items.

d) Actual dry weight of prey organisms. The dry weight of each prey species from a stomach is obtained by drying at 70°C to a constant weight. The weights of all prey species are then summed to give total dry weight consumed by each fish. The method does not take into account effects of digestion and gives an underestimate of the relative importance of well digested items.

e) Predicted dry weight of prey organisms. The original dry weight of prey is determined by measurement of some digestion resistant hard part. Relationships between the digestion resistant portion of the prey species and its original dry weight are obtained by field collection of prey species, measurement of the requisite part and then drying to a constant weight at 70°C. The method suffers from the disadvantage that, when large numbers of delicate animals have been consumed, the actual number present may be much greater than those actually identifiable, which may lead to an underestimate of dry weight consumed.

f) Energy value of prey. The pre-ingested size of prey can usually be determined by measurement of some digestion-resistant hard part. The calorific value of each prey organism is found by calorific value determinations on similarly-sized prey organisms of the same species collected in the study area. Calorific values of prey organisms which do not occur frequently can be obtained from published values for closely related species. The method suffers from the disadvantage that some calories are more readily available to the eel than others. Used in conjunction with data on growth rates, the information can give gross efficiency of food utilisation, i.e. the proportion of calories consumed in a year actually utilised in growth. If a value for assimilation efficiency is known, respiration may also be estimated. This aspect will be discussed in greater detail in a subsequent chapter. As the method appears to give the most precise information, it can be used to assess the merits of the easier methods outlined in a), b), c), d) and e).

Results were analysed with a Burroughs computer and four food analysis methods (a, d, e and f) were applied with respect to different eel size class and season. For ease of analysis

eels were grouped into season depending upon their month of capture. The sole criterion for allocation of seasons was water temperature (see Fig. 2). On this basis the seasons were:

Spring: September, October and November
Summer: December, January and February
Autumn: March, April and May
Winter: June, July and August

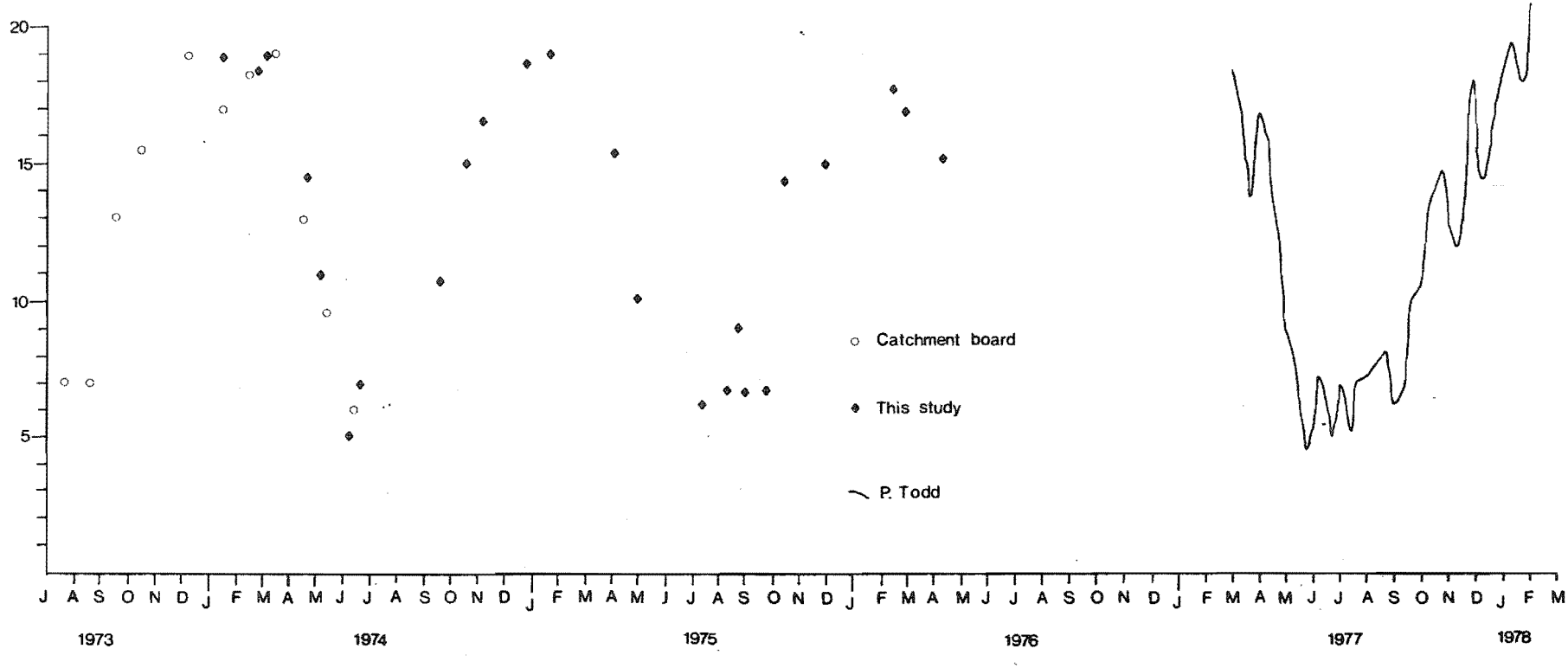


Fig. 2. Water temperatures in Lake Ellesmere.

## RESULTS AND DISCUSSION

### Size distribution

Eels were grouped into five cm size classes for the purpose of size frequency analysis. Because catch sizes varied with season, frequency was expressed as a percentage of the total number caught in that season (Fig. 3). There were insufficient eels (22) to present data for the winter sample.

The 487 eels caught ranged in size from 23.7 cm to 77.6 cm. Eels smaller than 30 cm were small enough to escape through the mesh of the net and were not often caught. This ease of escape of small eels masks any possible behavioural differences between large and small eels. Deelder (1970) considers small eels to be cryptozoic and relatively sedentary, which would reduce their chance of being captured in a fyke net (only 22 eels <30 cm were captured). Considerably fewer 30.1-35 cm (26) eels were caught than the 35.1-40.0 cm class (80). Eels in the 30.1-35 cm class were too big to escape through the mesh of the net so the reduced catch of that size class may be due to behavioural differences. It is reasonable to assume that the number of eels in each size class becomes less as the eels grow, so the smaller number of 30.1-35 cm eels should not truly reflect the population structure.

Sexually maturing eels are rarely captured because they migrate out of the population. The largest shortfin eel caught by Hobbs (1947) in Lake Ellesmere out of a sample of "many thousands" was 107 cm.

Comparison of the spring, summer and autumn length-frequency distributions with each other, and with the total for the whole sampling period, did not reveal any seasonal differences in the size-frequency distribution of the catch. No statistical tests were applied as the distributions appeared to be sufficiently similar not to warrant such a test. No differences were expected because the eel fishermen at Lake Ellesmere do not notice any change during the eel fishing season (K. Nordstromm, pers. comm.).

The size-frequency distributions do show that the fyke nets are size selective for middle-sized and large eels and that the size-frequency distribution of the sample obtained by them cannot be considered characteristic of the population. Because eels

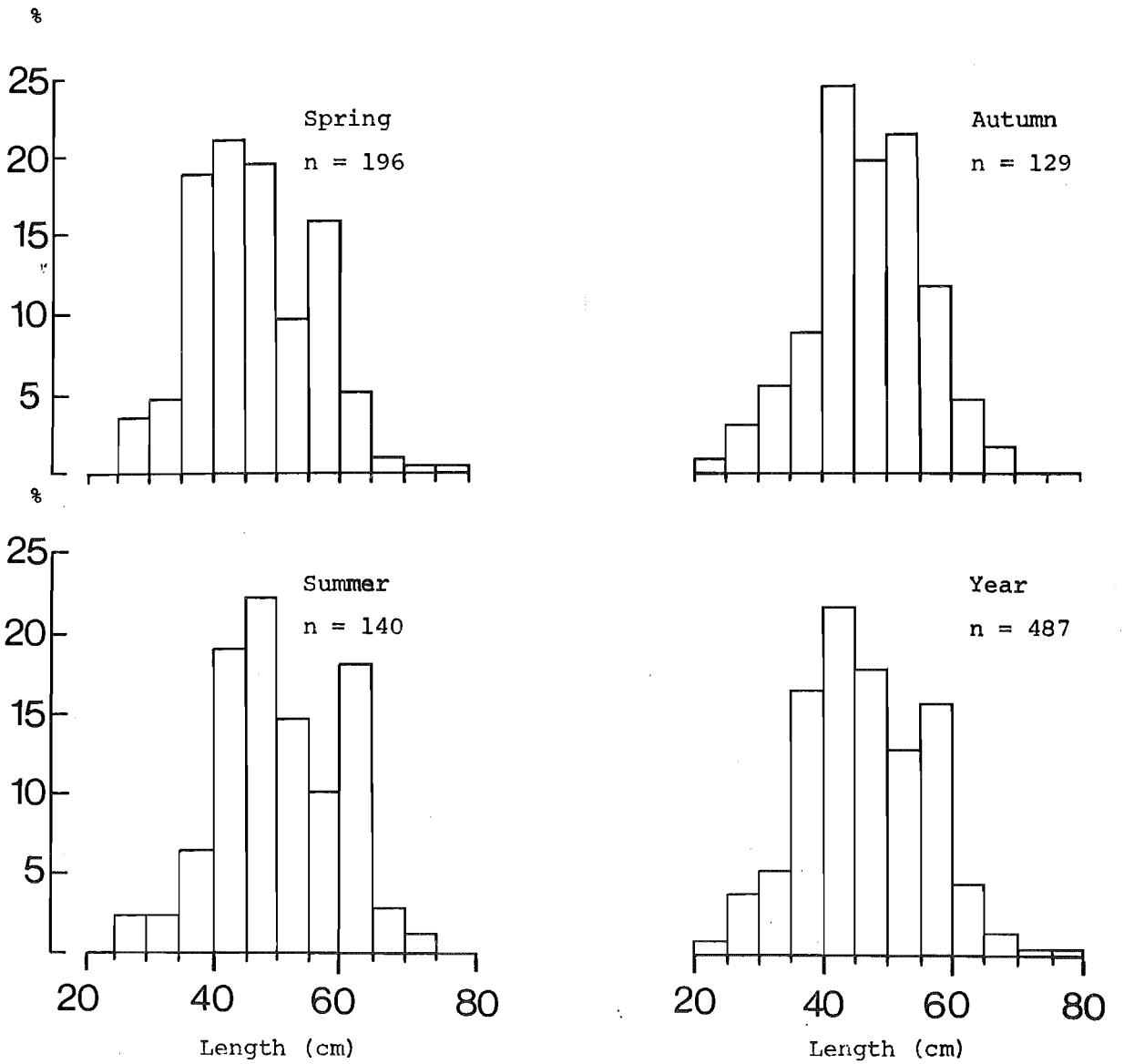


Fig. 3. Percentage size distribution of eel samples.

smaller than 23 cm were not caught, they were not included in this study.

Temporal distribution of eel catch

Analysis of catch data for each of the seasons shows some interesting trends (Table 2). Catch rates were highest in

Table 2. Seasonal distribution of eel catch.

| Season | Number of net nights | Number of eels caught | Catch rate (eels-net night) | Temp.* (°C) |
|---|---|---|---|---|
| Spring | 10 | 196 | 19.6 | 11.3 |
| Summer | 16 | 140 | 8.7 | 18.5 |
| Autumn | 18 | 129 | 7.2 | 12.1 |
| Winter | 28 | 22 | 0.8 | 6.5 |
| Year | 72 | 487 | 6.7 | 12.1 |

*Temperature averages from 1977 courtesy P. Todd.

spring and dropped to half this level in summer and autumn. The reason for this difference is not clear. If high temperatures alone were the determining factor summer should have the highest catch rate. If catch rates are a measure of feeding activity then the low catch rates in winter are not surprising. Draganik (1962) and Moore and Moore (1976) believe that the European eel, *A. anguilla*, stops feeding in winter. Sinha and Jones (1967b) suggest that *A. anguilla* does not feed at temperatures below 10-12°C. In New Zealand, Cairns (1941), Burnet (1969) and Hopkins (1970) all consider that eels either stop or reduce feeding in winter. Woods (1964) believes that eels stop feeding at temperatures below 6°C.

The high catch rates in spring are possibly activated by the increasing water temperature or increasing day length. Hopkirk *et al.* (1975) has shown that *A. a. schmidtii* is at its poorest condition in late winter-early spring due apparently to a long winter fast. They consider that the eels feed voraciously through spring while building up condition. A simplistic viewpoint would say that the eels are at their hungriest in spring, move around more looking for food and are thus more likely to be caught. A certain proportion of the eels will begin to mature sexually in summer and autumn and will probably

cease feeding (Cairns, 1941). This would remove a percentage of the fish from the population and may in part explain lower catch rates in summer and autumn. Inui and Oshima (1966) found that the lipid content of eels caught in late autumn was higher than that of a group caught in summer.

Low catch rates in winter do not necessarily mean that all feeding stops. They do suggest that active swimming in search of prey slows markedly but as some eel stomachs obtained in winter contained food some feeding does take place. The overall level of activity as revealed by catch rate is 1/10 that of summer and autumn and less than 1/20 of that in spring.

Of the 487 eels caught, 340 were caught by the nets at known times. The 3-hourly catches are shown in the frequency histograms in Fig. 4. Few fish were caught between 1200 h and 1800 h; only 4 were captured and all of these were in summer. It can be stated with a reasonable amount of certainty that active search behaviour and probably eel feeding does not begin until well after sunset. Activity is fairly uniform from 2100 h through to 0300 h, when it decreases slightly. From 0300 h to 0600 h activity is at a lower level. From 0600 h to 0900 h activity is minimal; only one fish was caught during this time interval. No fish were ever caught between 0900 h and 1200 h.

Times of sunrise and sunset (mean figures) are shown on the histograms and it can be seen that, although no eel activity starts until 2100 h, when it is completely dark, activity continues well beyond sunrise in spring and summer. Onset of night may be the stimulus to start feeding. Presumably eels which have been unsuccessful in feeding during the night continue for a certain time beyond dawn. A number of eels captured during daylight hours had empty stomachs but why they should limit their activity beyond 0900 is unknown. Jones and Evans (1960) found that the proportion of empty stomachs was much the same whether their electric fishing samples were taken by day or by night. Sinha and Jones (1975) argue that this shows that eels do not feed more actively at night. In the absence of information on gastric evacuation rates this is a dangerous conclusion. If it is accepted that fyke net catch rates are a measure of eel feeding activity my results show conclusively that *A. a. schmidtii* does feed more actively at night. Of the

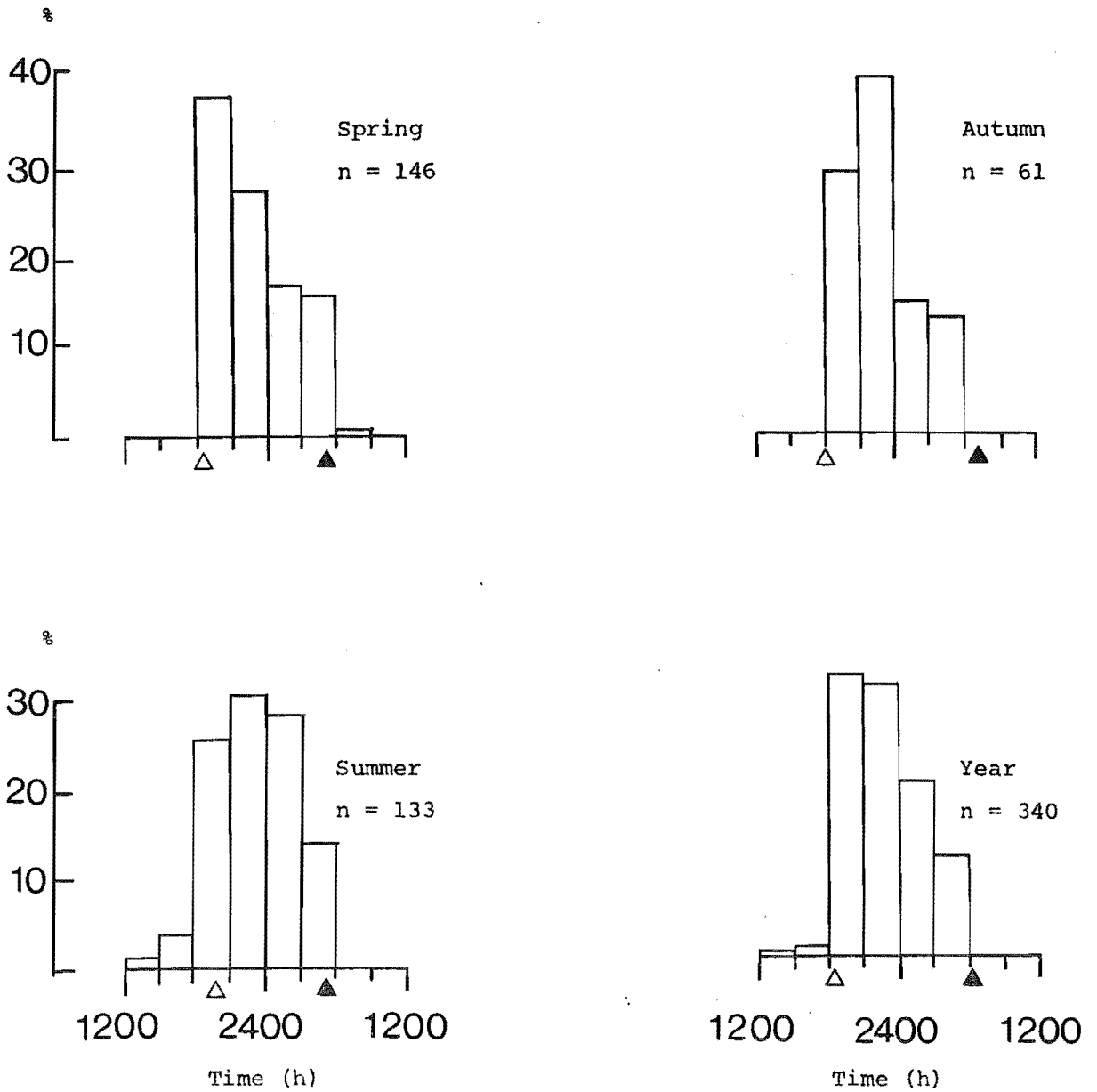


Fig. 4. Percentage catch distribution by capture time. Approximate mean time of sunrise is marked by ▲ and sunset by △.

340 eels for which capture times are known, 226 or 66% were caught at night. The number caught during the dark interval between 0300 and sunrise is unknown but would further increase the "dark catch" figures. Between the 0300 and 0600 sampling periods 70 eels were caught. As dawn occurred during this time a reasonable proportion of these eels were undoubtedly caught while it was still dark.

Catch rates were highly variable between different days as can be seen from Table 1. On 4 October 1974 no eels were captured in the two nets used but only two weeks later, on 18 October 1974, 31 eels were caught. Water temperatures were comparable; 14°C on the 4th and 15°C on the 18th. No weather or cloud cover records were kept because this would have entailed staying up all night if the observations were to be of value. Subsequent examination of phase of moon at times of sampling trips failed to show any correlation (this was not tested for significance as the plot appeared totally meaningless to the eye). From observation it appeared likely that more eels were caught on dark still nights than on bright windy nights. A full moon associated with full cloud cover may still produce high catch rates whereas a full moon without cloud cover may inhibit eel activity. Windy nights appeared to produce low catch rates probably because the small waves breaking up the shallow bank would have battered fish. Phase of moon has been shown in many studies to affect the migration of silver eels (Deelder, 1970) but presence of light is not necessary (Jens, 1952 to 1953 quoted in Deelder, 1970). Todd (1974) has shown that migration of silver eels in New Zealand is affected by the phase of the moon. Further study of feeding eel catch rates with respect to cloud cover and moon phase may show a significant relationship. The observations presented here are not based on analysis.

## FEEDING ANALYSES

### Visual estimate of fullness, and feeding periodicity

For the purpose of analysis eels were grouped into three size classes; ⩽40 cm, 40.1-50 cm, and >50 cm. As the analysis was intended to be as exhaustive as possible, the 5 cm size classes used for frequency distribution were not used, as the cells for each comparison would have become too small. Preliminary analysis sorted the eels into size classes and found the mean fullness index for each season (Table 3). It appears that

Table 3. Mean stomach fullness index by season and size class. Number of stomachs is given in brackets.

| Season | ⩽40 cm | 40.1-50 cm | >50 cm | All sizes |
|---|---|---|---|---|
| Spring | 1.00 (52) | 1.49 (80) | 3.09 (64) | 1.88 (196) |
| Summer | 3.12 (42) | 2.21 (52) | 2.65 (46) | 2.63 (140) |
| Autumn | 1.88 (24) | 1.07 (55) | 2.42 (50) | 1.74 (129) |
| Winter | 2.10 (10) | 0.00 (5) | 1.43 (7) | 1.41 (22) |
| Year | 1.95 (128) | 1.53 (192) | 2.70 (167) | 2.04 (487) |

in the case of the two smaller size classes fullness index reaches a maximum in summer and a minimum in autumn. The results for all eels suggest an increasing fullness index from winter to summer followed by a decrease in autumn.

Analysis with respect to size class and capture time showed an increasing fullness index towards daylight (Table 4).

Table 4. Mean stomach fullness index by size class and capture time. Number of stomachs is given in brackets.

| Capture time (h) | ⩽40 cm | 40.1-50 cm | >50 cm | All sizes |
|---|---|---|---|---|
| 1500 | 0 (0) | 0 (0) | 1 (1) | 1.0 (0) |
| 1800 | 0 (0) | 0 (2) | 0 (1) | 0 (0) |
| 2100 | 0.77 (30) | 0.78 (41) | 3.33 (39) | 1.68 (110) |
| 2400 | 1.59 (22) | 1.27 (44) | 2.30 (40) | 1.73 (106) |
| 0300 | 3.70 (27) | 1.92 (24) | 3.47 (19) | 3.03 (70) |
| 0600 | 4.29 (7) | 4.26 (27) | 2.60 (15) | 3.76 (49) |
| 0900 | 0.00 (0) | 0.00 (2) | 0.00 (1) | 0.00 (3) |
| 1200 | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| Day | 2.19 (86) | 1.80 (138) | 2.83 (116) | 2.25 (340) |

Capture time is defined as the hour nets are emptied, but covers the whole of the 3 hours prior to that time. These data suggest that the two smaller size classes feed through the night. The >50 cm size class exhibit no such trend of increasing fullness index but apparently do continue to feed until daylight as many caught at 0600 h contained food.

Finally, combined size classes were analysed with respect to season and hour of capture (Table 5).

Table 5. Mean stomach fullness index with respect to season and hour of capture. (All size classes pooled). Number of stomachs is given in brackets.

| Capture time (h) | Spring | | Summer | | Autumn | | Year | |
|---|---|---|---|---|---|---|---|---|
| 1500 | 0.00 | (0) | 0.00 | (1) | 0.00 | (0) | 0.00 | (1) |
| 1800 | 0.00 | (0) | 0.00 | (3) | 0.00 | (0) | 0.00 | (3) |
| 2100 | 1.61 | (57) | 1.71 | (34) | 1.84 | (19) | 1.68 | (110) |
| 2400 | 1.27 | (41) | 2.05 | (40) | 1.96 | (25) | 1.73 | (106) |
| 0300 | 2.38 | (24) | 3.54 | (37) | 2.67 | (9) | 3.03 | (70) |
| 0600 | 3.30 | (23) | 4.78 | (18) | 2.75 | (8) | 3.00 | (49) |
| 0900 | 1.00 | (1) | 0.00 | (0) | 0.00 | (0) | 1.00 | (1) |
| 1200 | 0.00 | (0) | 0.00 | (0) | 0.00 | (0) | 0.00 | (0) |
| Day | 1.90 | (146) | 2.68 | (133) | 2.13 | (61) | 2.25 | (340) |

It was hoped that these three sets of analyses would reveal any seasonal or size class changes in feeding success.

It would be tempting to draw conclusions from these data, but Jenkins and Green (1977) suggest that plotting the mean dry weight of food from captured fish against capture time does not give a correct view of feeding periodicity. They argue that in many cases the variance associated with samples is such that it completely masks any periodicity when the data is correctly analysed. Many workers use only mean dry weights from stomachs or mean fullness indices when calculating feeding periodicity. In the present study, wherever there are adequate samples (more than ten fish) mean fullness index appears to increase for the two smaller size classes throughout the night. Jenkins and Green (*loc. cit.*) would argue that this increase does not necessarily imply that feeding is primarily nocturnal but may be

an artifact due to incorrect analysis. To check this possibility each of the apparent trends noted in Tables 3, 4 and 5 was analysed for significance.

Fullness index could not be adequately analysed using parametric tests because the samples are not normally distributed (the fullness indices themselves are not on a linear scale). Instead they were analysed using the non-parametric Kruskal - Wallis test in which rank orders are used instead of actual values. No comparisons were made between size classes as it is felt that the value of fullness index as an indicator of feeding success may vary with the size of the fish. Tests were made for differences between mean ranked fullness indices for each size class, capture time and season. These were one tailed tests as the mean fullness index (M.F.I.) increases with capture time suggesting that later capture times should ensure fuller eels. Tests performed are given below (Table 6). *A posteriori* comparisons using z-scores (z-test) were also made but results are given only where the test for heterogeneity is significant. Significance is indicated wherever reached. Wherever all seasons or capture times are not represented in the tests the sample number was too small to use. These tests are not carried out on the mean fullness indices of the fish but are computed using ranks. While Mean Rank Score (M.R.S.) and Mean Fullness Index (M.F.I.) are comparable they are not identical. However, M.R.S. does give a reasonable estimate of M.F.I.

Only a few tests proved significant. The $\leqslant$40 cm summer eels (test 4) were heterogeneous and a z-test shows that M.R.S. of the fish captured at 0300 h was greater than those captured at 2100 h or 2400 h. Similarly the 0600 h fish were fuller than either the 2100 h or 2400 h fish. There was no significant difference however between fish caught at 2100 h and 2400 h or between fish caught at 0300 h and 0600 h. The 40.1-50 cm fish in the same season (test 5) show a similar but more positive trend. The M.R.S. of 2400 h fish is greater than 2100 h fish and M.R.S. of 0300 h fish is greater than 2100 h fish. There is no significant difference between 2400 h and 0300 h fish but 0600 h fish have significantly higher M.R.S. than either 2100 h, 2400 h or 0300 h fish. Comparison of M.R.S. for capture times over the whole year proved highly significant (test 9) and the z-tests showed that, apart from between 2100 h and 2400 h, there

Table 6. Results of Kruskal -Wallis tests and *a posteriori* comparisons using z-scores (z-tests).

| Group tested | Test for hetero-geneity | Signifi-cance level |
|---|---|---|
| 1. Spring ⩽40 cm | | |
| Capture times: 2100 2400 0300 h | 1.529 2 d.f. | N.S. |
| 2. Spring 40.1-50 cm | | |
| Capture times: 2100 2400 0300 0600 h | 2.080 3 d.f. | N.S. |
| 3. Spring >50.1 cm | | |
| Capture times: 2100 2400 0300 0600 h | 5.703 3 d.f. | N.S. |
| 4. Summer ⩽40 cm | | |
| Capture times: 2100 2400 0300 0600 h | 9.781 3 d.f. | 0.05 |

z-test

| h | 2400 | 0300 | 0600 |
|---|---|---|---|
| 2100 | N.S. | >0.01 | >0.01 |
| 2400 | - | >0.01 | >0.01 |
| 0300 | - | - | N.S. |

| 5. Summer 40.1-50 cm | | |
|---|---|---|
| Capture times: 2100 2400 0300 0600 h | 12.672 3 d.f. | >0.005 |

z-test

| h | 2400 | 0300 | 0600 |
|---|---|---|---|
| 2100 | >0.01 | >0.01 | >0.01 |
| 2400 | - | N.S. | >0.01 |
| 0300 | - | - | >0.05 |

| 6. Summer >50.1 cm | | |
|---|---|---|
| Capture times: 2100 2400 0300 0600 h | 0.683 3 d.f. | N.S. |

Table 6. continued

Table 6. continued

| | | | |
|---|---|---|---|
| 7. Autumn 40.1-50 cm | | | |
| Capture times: 2100 2400 0300 0600 h | 5.371<br>3 d.f. | N.S. | |
| 8. Autumn >50.1 cm | | | |
| Capture times: 2100 2400 h | 0.141<br>1 d.f. | N.S. | |
| 9. Year All fish | | | |
| Capture times: 2100 2400 0300 0600 h | 30.077<br>3 d.f. | >0.005 | |

z-test

| h | 2400 | 0300 | 0600 |
|---|---|---|---|
| 2100 | N.S. | >0.01 | >0.01 |
| 2400 | - | >0.01 | >0.01 |
| 0300 | - | - | >0.01 |

| | | | |
|---|---|---|---|
| 10. Year ⩽40 cm | | | |
| Capture time: Spring summer autumn winter | 14.503<br>3 d.f. | >0.01 | |

z-test

| | Summer | Autumn | Winter |
|---|---|---|---|
| Spring | N.S. | 0.01 | 0.01 |
| Summer | - | 0.01 | 0.01 |
| Autumn | - | - | N.S. |

| | | | |
|---|---|---|---|
| 11. Year 40.1-50 cm | | | |
| Capture time: Spring summer autumn winter | 15.720<br>3 d.f. | >0.01 | |

z-test

| | Summer | Autumn | Winter |
|---|---|---|---|
| Spring | 0.01 | 0.01 | 0.01 |
| Summer | - | 0.01 | 0.01 |
| Autumn | - | - | N.S. |

| | | | |
|---|---|---|---|
| 12. Year >50.1 cm | | | |
| Capture time: Spring summer autumn winter | 2.945<br>3 d.f. | N.S. | |

Table 6. continued

Table 6. continued

| | | | |
|---|---|---|---|
| 13. | 2100 h ⩽40 cm | | |
| | Capture time: Spring summer | 0.314<br>1 d.f. | N.S. |
| 14. | 2100 h 40.1-50 cm | | |
| | Capture time: Spring summer autumn | 3.261<br>2 d.f. | N.S. |
| 15. | 2100 h >50.1 cm | | |
| | Capture time: Spring summer autumn | 0.910<br>2 d.f. | N.S. |
| 16. | 2400 h ⩽40 cm | | |
| | Capture time: Spring summer | 1.144<br>1 d.f. | N.S. |
| 17. | 2400 h 40.1-50 cm | | |
| | Capture time: Spring summer autumn | 2.226<br>2 d.f. | N.S. |
| 18. | 2400 h >50.1 cm | | |
| | Capture time: Spring summer autumn | 2.701<br>2 d.f. | N.S. |
| 19. | 0300 h ⩽40 cm | | |
| | Capture time: Spring summer | 6.920<br>1 d.f. | >0.05 |

z-test

| | Summer |
|---|---|
| Spring | >0.01 |

| | | | |
|---|---|---|---|
| 20. | 0300 h 40.1-50 cm | | |
| | Capture time: Spring summer | 0.042<br>1 d.f. | N.S. |
| 21. | 0300 h >50.1 cm | | |
| | Capture time: Spring summer | 0.913<br>1 d.f. | N.S. |

Table 6. continued

Table 6. continued

| | | | |
|---|---|---|---|
| 22. | 0600 h 40.1-50 cm | | |
| | Capture time: Spring summer | 0.919<br>1 d.f. | N.S. |
| 23. | 0600 h >50.1 cm | | |
| | Capture time: Spring summer | 3.502<br>1 d.f. | N.S. |

was increasing fullness through the night.

These were the only tests to establish significant differences in M.R.S. between capture times. Tests between M.R.S. with respect to season showed a stronger trend. For eels ⩽40 cm (test 10) there is no significant difference between spring and summer, although test 19 shows a significant difference between fish caught at 0300 h. Autumn and winter fish are less full than spring and summer fish. The 40.1-50 cm size class feed with greater success in summer than in spring and with less success in autumn than either spring or summer. Winter levels are lower than spring or summer, but there is no difference between autumn and winter, due probably to the small size of the winter sample.

It appears from these data that most eels feed throughout the night and achieve their highest M.R.S. at 0600 h. They also feed with increasing success through spring and summer followed by a decrease in autumn and winter. Feeding probably stops for most eels at 0600 h - 0900 h which allows a maximum period of 12 hours before the onset of the next feeding period. The >50 cm size class do not show any significant differences in fullness index with respect to time of capture or season.

There is no published information on feeding rhythms in the eel, but there are a few studies of feeding periodicity of other fresh water fish, based upon either laboratory study or field observation. Darnell and Meierotto (1962) used degree of digestion of some standard reference item to determine time of ingestion. In this way they were able to find peak ingestion times in a wild population of *Ictalurus melas* (Black bullhead). Swenson and Smith (1973) used a similar method to determine feeding chronology of *Stizostedion vitreum vitreum* (walleye). They determined gastric evacuation rates of fish in laboratory experiments and extrapolated to the field situation. Steigenberger and Larkin (1974) determined activity of *Ptychocheilus oregonensis* (northern squawfish) by lifting trap nets at various hours of the day. While they were able to show that peak activity occurred at twilight and at night they were unable to show significant differences between weight of prey organisms removed from stomachs over a 24-hour period.

In New Zealand, Staples (1975) showed that complex changes took place in diel feeding activity and locomotory behaviour of

*Gobiomorphus breviceps* (upland bully). These changes depended upon the age class of the fish. Periods of higher feeding intensity appeared to follow periods of increased locomotory activity. Unfortunately so few eels were caught during the day in my study, presumably due to low locomotory activity, that no comparisons can be made between diurnal feeding intensity and locomotory behaviour. Griffiths (1975), using the method of Swenson and Smith (*loc. cit.*), showed that perch fed at a lower level at night and assumed this was due to perch being a visual feeder.

Feeding activity varies according to species but most studies show peak periods of activity during a 24 hour period. Lake Ellesmere eels are similar in this respect. Attempts were made to apply the method of Swenson and Smith to *A. a. schmidtii* to try to substantiate field-determined information and the results of this investigation are presented in Chapter 3.

Condition factor

A length/weight relationship for 373 eels was found by plotting log length against log weight and fitting a regression line to the data. This was done by computer fitting a Bartletts 3 group regression, which gave the equation

$$\log W = 3.0295 (\log L) - 5.8047$$

where W is weight in g and L is length in mm. F test for normality of variates = 2.577 with 123 d.f. (significant >0.001). A relationship such as this can be expressed in the form

$$W = aL^b$$

Where b is the slope and a is a constant.
This is often expressed as

$$K = W/L^b$$

in which K is known as "Fultons coefficient of condition". Substituting the value of b obtained from the regression equation we get

$$K = CW/L^{3.0529}$$

A constant C is introduced to make K close to unity. A computer programme was designed to determine K for each season and the mean for each season is shown in Table 7. These results suggest that eels are at their poorest condition in winter and improve through spring to a peak in late autumn followed by a steady decline during winter. This hypothesis was tested by a Kruskall-

Table 7. Mean condition factor for each season.

| | Condition factor | Number in sample |
|---|---|---|
| Spring | 1.006 | 190 |
| Summer | 0.997 | 80 |
| Autumn | 1.028 | 82 |
| Winter | 0.985 | 21 |

Wallace rank test. The test for heterogeneity was only significant at the 0.2 level but the z-tests were all highly significant. Results of z-tests are given in Table 8. The test for hetero-

Table 8. Results of z-tests between seasonal condition factors.

| | Summer | Autumn | Winter |
|---|---|---|---|
| Spring | >0.01 | >0.01 | >0.01 |
| Summer | - | >0.01 | N.S. |
| Autumn | - | - | >0.01 |

geneity between groups suggests that the seasonal samples are not significantly different. The z-test between pairs does achieve a high level of significance. Bigger sample sizes may have raised the significance of the heterogeneity test.

Griffiths (1975) found difficulty in determining condition factor in perch because of changes in gonad development. Because feeding eels divert minimal energy into gonad development, and because these results are based upon gutted eels, any change in condition factor is due almost entirely to the level of fat deposition. Inui and Oshima (1966) found that lipid levels were higher in eels caught in late autumn and Hopkirk (1975) found that summer levels of lipid in Lake Ellesmere eels were higher than levels in early spring. Moriarty (1972) attempted to determine values for b for eels from the Lake Corrib system, Northern Ireland. He was unable to demonstrate any significant differences between regression lines for samples from different years, but he does suggest that b increases to a maximum in July and drops in August. He attributes the drop in August (summer) to the departure of heavier individuals due to seasonal migration, but suggests that the prior increase is due to a build-up

of fat reserves after the winter hibernation. It is not known whether there is any seasonal migration of eels within Lake Ellesmere, although as length/frequency of the catch did not change throughout the sampling period, such a movement seems unlikely to be the case. The results of Inui and Oshima (1966), Moriarty (1972) and Hopkirk *et al.* (1975) all tend to support the claim that condition factor in Lake Ellesmere eels changes with season.

These results suggest that eel calorific input exceeds expenditure in spring and early autumn and expenditure exceeds input during late autumn and winter. In other words, during the colder period of the year eels lose weight. This suggestion has implications for subsequent growth studies. Any annual increment in weight for a particular size class masks a small drop in weight over winter which must be taken into account if all growth in any annual period is to be determined. This point is of particular importance in an energetics study when attempting to determine conversion efficiencies.

Frequency of occurrence and numerical methods

These two methods were used to compare both with each other, and with the dry weight and calculated calorific value of prey organisms. Results for all eels for the year are presented in Table 9.

Forty prey species were found in the stomachs during the sampling period, but of these only a few occurred frequently enough to be considered of great importance in the diet of the eel. Percentage occurrence and numerical occurrence are of equal value in indicating the most important food items, but percentage occurrence gives undue weight to the occurrence of infrequent small items. Numerical occurrence suffers because it does not give high enough weighting to bulky food items, such as fish. The two methods are useful in different ways and should be considered together as it requires little extra work to compute both methods for any given sample. However, as neither of the methods gives results as accurate as dry weights or calorific values, further comparison and discussion of these methods will not be made.

Table 9. Composition of the diet of Lake Ellesmere eels based upon 487 stomachs. Composition is expressed by the number of stomachs and percentage number of stomachs in which a species occurs, and by the percentage number of occurrences of all prey species and by total number of specimens. Where occurrence is below 1% an asterisk is used.

| | Number of stomachs | Percentage number of occurrence | Percentage numerical occurrence | Number |
|---|---|---|---|---|
| ANNELIDA | | | | |
| Oligochaeta | | | | |
| Lumbricidae | | | | |
| 1. *Lumbricus terrestris* | 3 | 1 | * | 50 |
| 2. Species A | 1 | * | * | 1 |
| 3. Species B | 2 | * | * | 28 |
| Polychaeta | | | | |
| Spionidae | | | | |
| 4. *Scolecolepides benhami* | 5 | 1 | * | 12 |
| ARTHROPODA | | | | |
| Crustacea | | | | |
| Mysidae | | | | |
| 5. *Tenagomysis chiltoni* | 46 | 9 | 2 | 322 |
| Amphipoda | | | | |
| Talitridae | | | | |
| 6. *Orchestia chilensis* | 1 | * | * | 9 |
| Eusiridae | | | | |
| 7. *Paracalliope fluviatilis* | 24 | 5 | 8 | 1 290 |
| Corophiidae | | | | |
| 8. *Paracorophium excavatum* | 10 | 2 | 2 | 305 |
| Isopoda | | | | |
| Idoteidae | | | | |
| 9. *Austridotea annectens* | 37 | 8 | 2 | 284 |
| Scyphidae | | | | |
| 10. *Porcellio scaber* | 4 | 1 | * | 71 |
| Insecta | | | | |
| 11. Collembola | 1 | * | * | 1 |

Table 9. continued

Table 9. continued

| | | | | |
|---|---|---|---|---|
| Odonata | | | | |
| Zygoptera | | | | |
| Coenagrionidae | | | | |
| 12. *Xanthocnemis zealandica* | 4 | 1 | * | 9 |
| Lestidae | | | | |
| 13. *Austrolestes colensonis* | 1 | * | * | 12 |
| Anisoptera | | | | |
| Corduliidae | | | | |
| 14. *Procordulia* sp. | 4 | 1 | * | 9 |
| Hemiptera | | | | |
| Corixidae | | | | |
| 15. *Sigara* sp. | 3 | 1 | * | 6 |
| Notonectidae | | | | |
| 16. *Anisops* sp. | 1 | * | * | 1 |
| Trichoptera | | | | |
| Leptoceridae | | | | |
| 17. *Triplectides cephalotes* | 8 | 2 | * | 15 |
| 18. *Oecetis unicolor* | 9 | 2 | * | 27 |
| Diptera | | | | |
| Chironomidae | | | | |
| 19. *Psectrotanypus antarcticus* | 8 | 2 | * | 52 |
| 20. *Chironomus zealandicus* (larvae) | 57 | 12 | 18 | 3 106 |
| 21. *Chironomus zealandicus* (pupae) | 25 | 5 | 1 | 188 |
| 22. *Chironomus zealandicus* (adult) | 5 | 1 | * | 11 |
| 23. *Polypedilum* sp. | 1 | * | * | 1 |
| Tipulidae | | | | |
| 24. *Erioptera confluens* | 1 | * | * | 1 |
| 25. *Paralimnophora skusei* | 1 | * | * | 1 |
| Dolichopodidae | | | | |
| 26. Species A | 1 | * | * | 1 |
| Ephydridae | | | | |
| 27. *Ephydrella* sp. (larva) | 1 | * | * | 1 |
| 28. *Ephydrella* sp. (adult) | 1 | * | * | 5 |

Table 9. continued

Table 9. continued

| | | | | |
|---|---|---|---|---|
| Muscidae | | | | |
| 29. Species A | 1 | * | * | 1 |
| 30. Species B | 2 | * | * | 2 |
| Coleoptera | | | | |
| Scarabeidae | | | | |
| 31. *Costelytra* sp. (larvae) | 1 | * | * | 1 |
| 32. *Costelytra* sp. (adult) | 2 | * | * | 2 |
| Dytiscidae | | | | |
| 33. *Rhantus pulverosus* (larvae) | 1 | * | * | 1 |
| Lepidoptera | | | | |
| 34. *Nymphula nitens* | 3 | 1 | * | 5 |
| MOLLUSCA | | | | |
| Gastropoda | | | | |
| Hydrobiidae | | | | |
| 35. *Potamopyrgus antipodarum* | 111 | 23 | 63 | 10 767 |
| Physidae | | | | |
| 36. *Physa* sp. | 3 | 1 | 1 | 88 |
| Planorbidae | | | | |
| 37. *Gyraulus* sp. | 1 | * | * | 60 |
| 38. Limacidae | 1 | * | * | 21 |
| VERTEBRATA | | | | |
| Osteich thyes | | | | |
| Galaxiidae | | | | |
| 39. *Galaxias maculatus* | 8 | 2 | * | 9 |
| Retropinnidae | | | | |
| 40. *Retropinna retropinna* | 22 | 5 | * | 29 |
| Cyprinidae | | | | |
| 41. *Carassius carassius auratus* | 2 | * | * | 2 |
| Pleuronectidae | | | | |
| 42. *Rhombosolea* sp. | 1 | * | * | 1 |
| Eleotridae | | | | |
| 43. *Gobiomorphus cotidianus* | 24 | 5 | * | 30 |
| Other | | | | |
| 44. Fish eggs | 2 | * | ? | ? |

Actual dry weight of food organisms

For the purpose of this analysis the eel samples were separated by season of capture. Further subdivision with respect to size class was intended if the results of this analysis, and those from predicted dry weights of prey organisms, proved comparable. It subsequently proved necessary to use a combination of methods to calculate calorific values from dry weights of prey organisms. Neither predicted dry weight of prey organisms or actual dry weight could be used on its own, so discussion here is restricted, until data from the predicted dry weight analysis is presented. (Tables 16, 17 and 18 give comparisons between the two methods).

In spring, *P. antipodarum* (36.1%) contributed the most weight to the diet of the eel, followed by *R. retropinna* (29.5%), *G. cotidianus* (28%) and *A. annectens* (3.1%). The contribution of all other food species was negligible. In summer *P. antipodarum* (40.6%) was again the dominant food organism by dry weight but *C. zealandicus* larvae (25%) were second in importance. *G. cotidianus* (14%), *G. maculatus* (12.9%) and *R. retropinna* (3.2%) also made substantial contributions. In autumn *G. cotidianus* (36.3%) gave the greatest dry weight contribution followed by *P. antipodarum* (22%), *R. retropinna* (18.1%), *T. chiltoni* (6.1%) and *C. zealandicus* (5.8%). Contributions from all other species constituted less than 10% of the diet by weight. Of particular interest are seasonal changes in the relative abundance of *C. zealandicus* larvae which reach a peak in summer, coinciding with the emergence and subsequent swarming of *C. zealandicus* adults. *T. chiltoni* is most important in autumn. *G. maculatus* makes its greatest contribution in summer. The relative importance of the other food species with respect to dry weight appears to remain fairly constant.

It was evident, while analysing this data, that the contribution of fish to the diet was being underestimated by this method. Further analysis was therefore not attempted as enough information had been gained to demonstrate the use of the method in comparing the relative dry weight contributions of dietary items.

Predicted dry weight of food organisms

Seasonal field collections were made of *G. cotidianus*, *P. antipodarum*, *T. chiltoni* and *A. annectens* and occasionally collections were made of other species. In each case a relationship was established between some digestion resistant portion of the animal and its dry weight, by computer fitting a regression line using Bartletts 3 group method. In the case of *P. antipodarum* the regression lines were fitted to mean dry weights by grouping 50-60 individuals of similar length. Results are presented in Tables 10-16. A regression was also fitted for telson length of *A. annectens* on total length so that dry weights could be determined for fragmented specimens in which the telson remained intact. *A. annectens* was rarely fragmented, so the added error caused by not establishing telson length/dry weight relationships is small.

The equation was

$$L = 3.29\ T.L. - 0.1628$$

| F test | Significance |
|---|---|
| 1.595 | >0.1 |

where L is total length in mm and T.L. is telson length.

In all cases where more than one season was involved the regression lines were compared using t-tests to test for differences in slope and for differences between constants. In most cases there was no significant difference between slopes, but differences in constants were frequent, which implies that the lines belong to the same family of curves. As the length/dry weight equation was used solely for the season it described, significant differences between lines are not important. If, however, no differences between the regressions had been found, the use of one regression for all seasons would have been valid. No regression line was fitted to data for autumn *P. antipodarum* so results were obtained by interpolation from the summer and winter equations. For broken *P. antipodarum* no aperture length/dry weight relationship was established for autumn and winter animals, so total length was determined from aperture length using a regression from 435 *P. antipodarum* aperture length/total length measurements.

The equation was

$$L = 2.884\ A.L. - 0.7066$$

| F test | Significance |
|---|---|
| 1.049 | 0.05 |

where L is total length in mm and A.L. is aperture length in mm.

Table 10. Regression equations of carapace length on dry weight for *T. chiltoni*. W is weight in g. L is length in mm

| Season | Regression equation | Number of data pairs | F test for normality of variates | Significance level |
|---|---|---|---|---|
| Spring | W = 0.0028 L - 0.0047 | 302 | 4.804 | >0.001 |
| Summer | W = 0.0017 L - 0.0030 | 260 | 4.767 | >0.001 |
| Autumn | W = 0.0022 L - 0.0042 | 303 | 20.493 | >0.001 |
| Winter | W = 0.0021 L - 0.0037 | 157 | 4.330 | >0.001 |

Table 11. Regression equations of length on dry weight for *A. annectens*. W is weight in g. L is length in mm.

| Season | Regression equation | Number of data pairs | F test for normality of variates | Significance level |
|---|---|---|---|---|
| Spring | log W = 2.4004 log L - 4.4473 | 101 | 2.207 | >0.05 |
| Summer | log W = 2.4774 log L - 4.5775 | 227 | 4.378 | >0.001 |
| Autumn | log W = 1.8395 log L - 3.9072 | 209 | 4.096 | >0.001 |
| Winter | log W = 2.3926 log L - 3.5060 | 170 | 3.167 | >0.001 |

Table 12. Regression equations of length on dry weight for *P. antipodarum*. W is weight in g. L is longest shell dimension in mm.

| Season | Regression equation | Number of data pairs | F test for normality of variates | Significance level |
|---|---|---|---|---|
| Spring | log W = 2.1524 log L - 3.9316 | 5 | 5.701 | >0.05 |
| Summer | log W = 2.5112 log L - 4.1308 | 5 | 5.092 | 0.05 |
| Winter | log W = 2.2399 log L - 3.8349 | 14 | 13.290 | >0.001 |

Table 13. Regression equations of aperture on dry weight for *P. antipodarum*. W is weight in g. L is aperture of shell in mm.

| Season | Regression equation | Number of data pairs | F test for normality of variates | Significance level |
|---|---|---|---|---|
| Spring | log W = 3.0303 log L - 3.4131 | 5 | 5.701 | >0.05 |
| Summer | log W = 2.9123 log L - 3.3422 | 5 | 5.092 | 0.05 |

Table 14. Regression equations of length on dry weight for *G. cotidianus*. W is weight in g. L is standard length in mm.

| Season | Regression equation | Number of data pairs | F test for normality of variates | Significance level |
|---|---|---|---|---|
| Spring | log W = 3.5732 log L - 2.7944 | 65 | 1.720 | 0.1 |
| Summer | log W = 3.3152 log L - 2.6202 | 45 | 15.232 | >0.001 |
| Autumn | log W = 3.6424 log L - 2.8046 | 38 | 1.486 | 0.2 |
| Winter | log W = 3.5610 log L - 2.7922 | 112 | 1.677 | 0.5 |

Table 15. Regression equation of length on dry weight for *R. retropinna* and *G. maculatus*. W is weight in g. L is standard length in mm.

| Species | Regression equation | Number of data pairs | F test for normality of variates | Significance level |
|---|---|---|---|---|
| *R. retropinna* | logW = 2.5564 logL - 4.9144 | 20 | 1.710 | 0.25 |
| *G. maculatus* | logW = 4.5057 logL - 8.8575 | 15 | 1.377 | 0.25 |

Using criteria given by Robb (1966), it was established that nearly all (3101 out of 3106) *C. zealandicus* larvae ingested by the eels were 4th instar. A mean dry weight for 4th instar larvae was obtained from 96 specimens. Pupae of *C. zealandicus* were assumed to have a similar dry weight. Dry weights of *P. fluviatilis* were determined by weighing 1000 animals of various sizes and determining the mean value. For all other prey

Table 16. Dry weights of *C. zealandicus* and *P. fluviatilis*. Number of specimens given in brackets.

| Species | Mean dry weight (g) | |
|---|---|---|
| *C. zealandicus* larvae | 0.00117 | (96) |
| *P. fluviatilis* | 0.0003 | (1000) |

organisms actual dry weight was used, instead of predicted weight, except in the case of large well digested organisms. For these specimens an estimate of dry weight, based on the actual dry weight, was made. As the contribution of organisms other than those for which length/dry weight relationships were obtained was minimal, the subjectivity introduced by such procedures hardly affects the overall result.

Direct comparison of actual dry weights of food organisms with those predicted was not possible for the first 60 fish caught because only dry weights of prey were determined and no measurements were taken. Tables 17, 18 and 19 show comparisons for all other fish between actual and predicted dry weights for organisms obtained in spring, summer and autumn. It can be seen that the contribution of fish as food is underestimated when actual weights are used. In spring (Table 17) *R. retropinna* contributes 29.5% by actual weight, and 40.5% by predicted weight; *G. cotidianus* contributes 28% by actual weight and 37.9% by predicted weight. A similar pattern is evident in summer and autumn.

The predicted dry weights of *P. antipodarum* are, however, much less than the actual weights (15.7% c.f. 36% in the spring sample, 25.5% c.f. 40.6% in summer and 13% c.f. 22% in autumn). *C. zealandicus* is very similar; in summer the predicted weight is 17.5% c.f. 25% for the actual weight.

Table 17. Dry weights and predicted dry weights (from length-dry weight relationships) of food species from stomachs of spring eels. Percentage of total given in brackets.

| Species | Actual weight (g) | Predicted weight (g) |
|---|---|---|
| *T. chiltoni* | 0.2586 (0.7) | 0.3516 (0.7) |
| *P. fluviatilis* | 0.3902 (1.0) | 0.4118 (0.9) |
| *A. annectens* | 1.1821 (3.1) | 1.4451 (3.0) |
| *C. zealandicus* larvae | 0.0756 (0.2) | 0.0898 (0.2) |
| *P. antipodarum* | 13.7353 (36) | 7.3999 (15.7) |
| *G. maculatus* | 0.2504 (0.7) | 0.2566 (0.5) |
| *R. retropinna* | 11.2226 (29.5) | 19.0630 (40.5) |
| *G. cotidianus* | 10.6471 (28) | 17.8503 (37.9) |
| Other | 0.2909 (0.7) | 0.2239 (0.5) |
| Total | 38.0527 | 47.0920 |

Table 18. Dry weights and predicted dry weights (from length-dry weight relationships) of food species from stomachs of summer eels. Percentage of total given in brackets.

| Species | Actual weight (g) | Predicted weight (g) |
|---|---|---|
| *T. chiltoni* | 0.0807 (0.5) | 0.1123 (0.7) |
| *C. zealandicus* larvae | 4.2861 (25) | 2.6532 (17.5) |
| *C. zealandicus* pupae | 0.1710 (1.0) | 0.0339 (0.2) |
| *P. antipodarum* | 6.9076 (40.6) | 3.8520 (25.5) |
| *G. maculatus* | 2.1936 (12.9) | 2.60 (17.1) |
| *R. retropinna* | 0.5479 (3.2) | 1.250 (8.2) |
| *G. cotidianus* | 2.3752 (14) | 4.1285 (27.3) |
| Others | 0.2002 (1.2) | 0.2290 (1.5) |
| Total | 17.0258 | 15.1355 |

Table 19. Dry weights and predicted dry weights (from length-dry weight relationships) of food species from stomachs of autumn eels. Percentage of total given in brackets.

| Species | Actual weight (g) | Predicted weight (g) |
|---|---|---|
| *T. chiltoni* | 0.8119 (6.1) | 0.8421 (4.8) |
| *A. annectens* | 0.0920 (0.7) | 0.1003 (0.6) |
| *P. antipodarum* | 2.9167 (22) | 2.2754 (13) |
| *G. maculatus* | 0.4237 (3.2) | 0.9200 (5.2) |
| *R. retropinna* | 2.4054 (18.1) | 6.2100 (35.3) |
| *Carassius c. auratus* | 0.5279 (4.0) | 0.5400 (3.1) |
| *G. cotidianus* | 5.0877 (38.3) | 5.7719 (32.9) |
| Other | 0.2263 (1.7) | 0.2365 (1.3) |
| Total | 13.2546 | 17.5640 |

There are two possible reasons for this result. The organisms collected for the length/weight relationships values may not have been characteristic of the population on which the eels were feeding. Or the number of animals identified and measured from the stomachs was less than the actual number present. The latter explanation is the most likely, as in many cases when few *P. antipodarum* or *C. zealandicus* had been eaten the predicted weights were greater than the actual. The larger the number of organisms counted in the stomach the larger was the discrepancy between the two measurements. This discrepancy questions the validity of using predicted dry weights instead of actual weights for small numerous items. On the other hand actual dry weights demonstrably underestimated the importance of large food organisms.

It appears from the data presented here that neither method may be used with complete confidence. Choice of method may depend upon the diet of the species studied. Piscivorous species are probably best studied using the predicted weights. Carnivorous feeders which feed upon small organisms in large numbers may best be studied using actual weights. In some species diet may change with size of eel and season, which is the case in this study. In such cases the use of both methods is recommended.

Energy value of prey

Calorific values were determined for the most important food organisms (Tables 20-25). These results show that differences in calorific value of any prey organism may occur depending upon the season of capture or the size class involved. Most authors present results in calories, but to conform with metric terminology all results have been converted to joules (all calorific values are in terms of joules/g dry weight). Cummins and Wuycheck (1971) suggest that only differences of between 2093.5 and 4187 joules/g dry weight may be considered significant in most ecological studies because of the variance encountered in sampling programmes. *T. chiltoni* values (Table 21) ranged from 18787 j/g for 3.05-3.50 mm carapace length caught in autumn and winter to 22178 j/g for animals with carapace length greater than 3.55 mm caught in summer. These results give a total range of 3391 j/g which is probably a significant difference according to Cummins and Wuycheck's criteria (*loc. cit.*). The isopod *A. annectens* (Table 22) showed the greatest range in calorific value with respect to size class, from 10069 j/g for individuals longer than 12.55 mm caught in spring to 16325 j/g for individuals less than 9.0 mm caught in autumn. This range of 6256 j/g arises from two factors; firstly the exoskeleton becomes proportionately much thicker and heavier as the animals grow, hence calorific value decreases proportionately as much of this material is inorganic, and secondly there is strong sexual dimorphism. Nearly all individuals longer than 12 mm are males whereas in autumn, when sexual maturity is reached (P. Ryan, *in prep.*) nearly all <9.0 mm isopods are females which contain large amounts of fat in the form of stored eggs or young in the marsupium. Males release their sperm at this time and might be expected to decrease in calorific value. The highest calorific figure for this

Table 20. Calorific values of *P. fluviatilis* and *C. zealandicus*. Results are given ±1 standard error.

| Species | Size | Calorific value (joules/g dry weight) |
|---|---|---|
| *P. fluviatilis* | Average of all sizes | 17568 ± 250 |
| *C. zealandicus* | 4th instar | 17592 ± 190 |

Table 21. Seasonal variation in calorific value (joules/g ± standard error where applicable) of *Tenagomysis chiltoni*. n = number of samples (pooled sample from several specimens).

Carapace length

| (mm) | <2.00 | 2.05-2.50 | 2.55-3.00 | 3.05-3.50 | 3.55-4.00 | 4.05-4.50 | >4.50 |
|---|---|---|---|---|---|---|---|
| Spring | - | 21127<br>n = 2 | 20788<br>n = 2 | 21136<br>n = 2 | 21467 ± 80<br>n = 3 | 21994<br>n = 2 | - |
| Summer | 21525<br>n = 1 | | 21759<br>n = 2 | 21735<br>n = 2 | 22178<br>n = 1 | | |
| Autumn | - | 20650 ± 480<br>n = 3 | | 18787<br>n = 2 | 21002<br>n = 2 | 20910<br>n = 1 | 20646<br>n = 1 |
| Winter | - | 21789<br>n = 1 | | 18787<br>n = 1 | 20344<br>n = 1 | | |

Table 22. Seasonal variation in calorific value (joules/g ± standard error where applicable) of *Austridotea annectens*. n = number of samples (pooled sample from several specimens).

| Size (mm) | <7.00 | 7.05-7.55 | 7.55-8.00 | 8.05-8.50 | 8.55-9.00 | 9.05-9.50 | 9.55-10.00 | 10.05-10.50 | 10.55-11.00 | 11.05-11.50 | 11.55-12.00 | 12.05-12.50 | 12.55-13.00 | >13.05 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Spring | 15630 n = 1 | | | | 13632 n = 1 | 13633 n = 1 | 12900 n = 1 | 13511 n = 1 | 10090 n = 1 | | | | 10069 n = 2 | |
| Summer | 14575 n = 1 | 14391 n = 1 | 14152 n = 1 | 13699 n = 1 | 14118 ± 48 n = 3 | 13633 n = 2 | 14085 n = 2 | 13779 n = 1 | | | | | - | |
| Autumn | 16325 ± 280 n = 3 | | | | | 15952 n = 3 | | 14633 n = 2 | | 13813 n = 4 ± 190 | | 13603 n = 4 ± 120 | | - |
| Winter | 14462 n = 2 | | | | | 13913 n = 2 | 13067 n = 1 | 10936 n = 2 | | | | | 10836 n = 1 | |

Table 23. Seasonal variation in calorific value (joules/g ± standard error) of *Potamopyrgus antipodarum*. n = number of samples (pooled sample from several specimens).

| Season \ shell length (mm) | <3.00 | 3.10-3.50 | 3.60-4.00 | 4.10-4.50 | 4.50-5.00 | >5.10 |
|---|---|---|---|---|---|---|
| Spring | 5263 ± 481<br>n = 3 | 5447 ± 573<br>n = 6 | | 6209<br>n = 2 | 6615<br>n = 2 | 5995<br>n = 1 |
| Summer | 4706 ± 420<br>n = 3 | 4706 ± 510<br>n = 3 | | 4689<br>n = 2 | 4806<br>n = 1 | 6217<br>n = 1 |
| Winter | - | - | - | 3660.1<br>n = 1 | 3678<br>n = 2 | 3567<br>n = 1 |

Table 24. Seasonal variation in calorific value (joules/g ± standard error) of *G. cotidianus*. n = number of samples (pooled sample from several specimens).

| length (cm) | <3.00 | 3.10-4.00 | 4.10-5.00 | 5.10-6.00 | 6.10-7.00 | 7.10-8.00 | >8.10 |
|---|---|---|---|---|---|---|---|
| Spring | 20826 ± 240<br>n = 3 | 20750 ± 320<br>n = 6 | 20876 ± 140<br>n = 6 | 21387 ± 135<br>n = 5 | 20717 ± 100<br>n = 6 | 20533 ± 120<br>n = 6 | - |
| Summer | 21356 ± 500<br>n = 3 | 20348 ± 452<br>n = 6 | 20658 ± 420<br>n = 5 | 20830 ± 212<br>n = 7 | 21018 ± 322<br>n = 5 | - | - |
| Autumn | - | 21743 ± 871<br>n = 5 | 21288 ± 630<br>n = 7 | 21708 ± 519<br>n = 6 | 22664 ± 227<br>n = 7 | 22698 ± 553<br>n = 7 | |
| Winter | 20747 ± 588<br>n = 5 | 20145 ± 920<br>n = 5 | 21722 ± 981<br>n = 5 | 19683 ± 459<br>n = 5 | 21184 ± 892<br>n = 6 | 21642 ± 639<br>n = 7 | 22480 ± 277<br>n = 6 |

species is 62% higher than the lowest, which is an extremely large variation. *P. antipodarum* calorific values (Table 23) also range widely in value. The highest figure obtained was 6615 j/g for 4.1-4.5$_{mm}$animals sampled in spring and the lowest was only 3567 j/g for animals greater than 5.1 mm caught in winter. The extent of this range may be due to changes in shell weight or to accumulation of sexual products or both. The changes show no consistent variation between size classes but do show variations between seasons. Winter values are much lower than summer or spring, and spring is generally higher than summer. Shells of *P. antipodarum* are highly variable in form and large differences in length/dry weight relationships between sample areas may be reflected in the calorific values obtained. Values for *G. cotidianus* (Table 24) varied from 19683 j/g for 5.1-6.0 cm fish caught in winter to 22698 j/g for 7.1-8.0 cm fish caught in autumn. This range of 3015 j/g is probably a significant difference, according to Cummins and Wuycheck (*loc. cit.*). It should be stressed that Cummins and Wuycheck only apply this criterion to a whole ecosystem study. The differences obtained for *G. cotidianus* are significant when the study is concerned only with *G. cotidianus*.

Values for *R. retropinna* and *G. maculatus* (Table 25) are similar to the *G. cotidianus* values.

Table 25. Calorific value (joules/g ± standard deviation) of *R. retropinna* and *G. maculatus* (pooled from several specimens).

| Species | Calorific value (joules/g dry weight) | Number of samples |
|---|---|---|
| *R. retropinna* | 20 773 ± 164 | n = 5 |
| *G. maculatus* | 22 114 ± 188 | n = 5 |

Overall these results are comparable to values given by Cummins and Wuycheck (1971) and Prus (1975) but vary considerably from figures given by Sitaramaiah (1967). Sitaramaiah obtained values of 24661 j for *Chironomus* larvae compared with 17592 j in my study, and values of 16245 j for the fish *Gobius giuris* compared with values of 21000 j for *G. cotidianus*. These differences may not only be due to variations between organisms

but may also depend upon the method used by Sitaramaiah, who determined the nitrogen content of each organism and converted these figures to calorific values. Willner (1972) determined calorific values of *Asellus aquaticus* and obtained mean figures of 14185 j, which compares favourably with figures for calorific value obtained from *Austridotea annectens* in my study. Willner also determined calorific values of *Chironomus plumosus* and his mean figure of 17802 j/g compares closely with the figure of 17592 j/g for *Chironomus zealandicus*. Kelso (1973) showed substantial seasonal changes in calorific value of *Perca flavescens* (yellow perch). Values ranged from 20122 j/g to 22421 j/g which are similar to the values for *G. cotidianus*, *R. retropinna* and *G. maculatus* in this study. *Gammarus lacustris* gave a value of 16308 j/g which is considerably lower than the 17568 j/g for *P. fluviatilis*. Rodgers and Qadri (1977) show significant seasonal changes in *Asellus* sp., *Gammarus fasciatus* and Chironomidae spp. Values for *Asellus* ranged from 13616 j/g to 16668 j/g. *Gammarus fasciatus* ranged from 16509 j/g to 17828 j/g and Chironomidae spp. (larvae) from 17485 j/g to 19833 j/g. Values for *A. annectens*, *P. fluviatilis* and *C. zealandicus* in this study are similar.

Using the values from Tables 20-25, in conjunction with the dry weights obtained for the prey organisms from the regression equations, it was possible to calculate the total calorific value of the stomach contents of each eel. Unfortunately the problems outlined earlier of actual dry weight being an underestimate for large items and predicted dry weight being an underestimate for small food items were encountered. It was decided, therefore, to use the largest dry weight value available for any organism; in the case of most small organisms this was the actual dry weight, in the case of most large organisms the predicted dry weight was used. This method combines the advantages of both the methods outlined, but with none of the disadvantages. It does require slightly more work to compute but produces a result which is more accurate than either predicted or actual dry weight. Using this method, the dry weight for each food organism was calculated and the calorific value for the size class determined from one of the tables. When actual dry weight was used the contribution to total weight of each size class was not known, so an average value for that season of all

size classes was applied. The results of these calculations are presented for each season, each size class of eels, all eels and the whole year in Appendix 1 (Tables A.1-A.17). For ease of comparison and discussion the calorifically most important food items for each size class of eel and season are presented in Figs 5-9 in the form of pie diagrams, together with pie diagrams of their dry weights. Fig. 5 shows the percentage contribution of the major food organisms in spring expressed both calorifically and as dry weight for the three size classes of eel. The most obvious difference between size classes is the relative lack of fish in the diet of ⩽40 cm eels; in calorific terms, *G. maculatus* contributed only 13.3% of the diet. *A. annectens* and *P. antipodarum* were both important (20.3% each). Of interest is the great difference in the relative importance of *P. antipodarum* when expressed in dry weight or in calorific terms. Studies basing the relative importance on dry weight (or volume) are likely to be misleading when small snails are involved. By weight, *P. antipodarum* contributed 45.1% of the diet of ⩽40 cm eels and *C. zealandicus* is also of importance. In the next size class the relationships change markedly. Invertebrates contribute only about 15% of the diet, compared with 85% by the fish, *G. cotidianus* (46.8%) and *R. retropinna* (38%). The >50.1 cm size class shows an even greater dependence upon fish, *G. cotidianus* (44%) and *R. retropinna* (46%) making up the bulk of the diet. *P. antipodarum* contributes only 6.7% calorifically but 23.5% in terms of dry weight.

In summer (Fig. 6) the diet of ⩽40 cm eels is still predominantly invertebrate. *C. zealandicus* larvae become calorifically the most important food item with 36.1%, closely followed by *R. retropinna* (34.5%), whereas *A. annectens* (4.4%) becomes less important and terrestrial oligochaetes contribute 11.3%. The input of terrestrial oligochaetes appears to be associated with the occasional inundation of pasture around the lake shore. Smaller eels appear to be able to take better advantage of such events, perhaps because they expose themselves to air less in shallow water than do large eels. *C. zealandicus* larvae are the most important item in the diet of 40.1-50 cm eels giving 59.8% of the total calorific input and 44.2% by dry weight. Terrestrial oligochaetes contribute 13.3% calorifically and *P. antipodarum* is again of importance with 12.2%. *G. cotidianus*

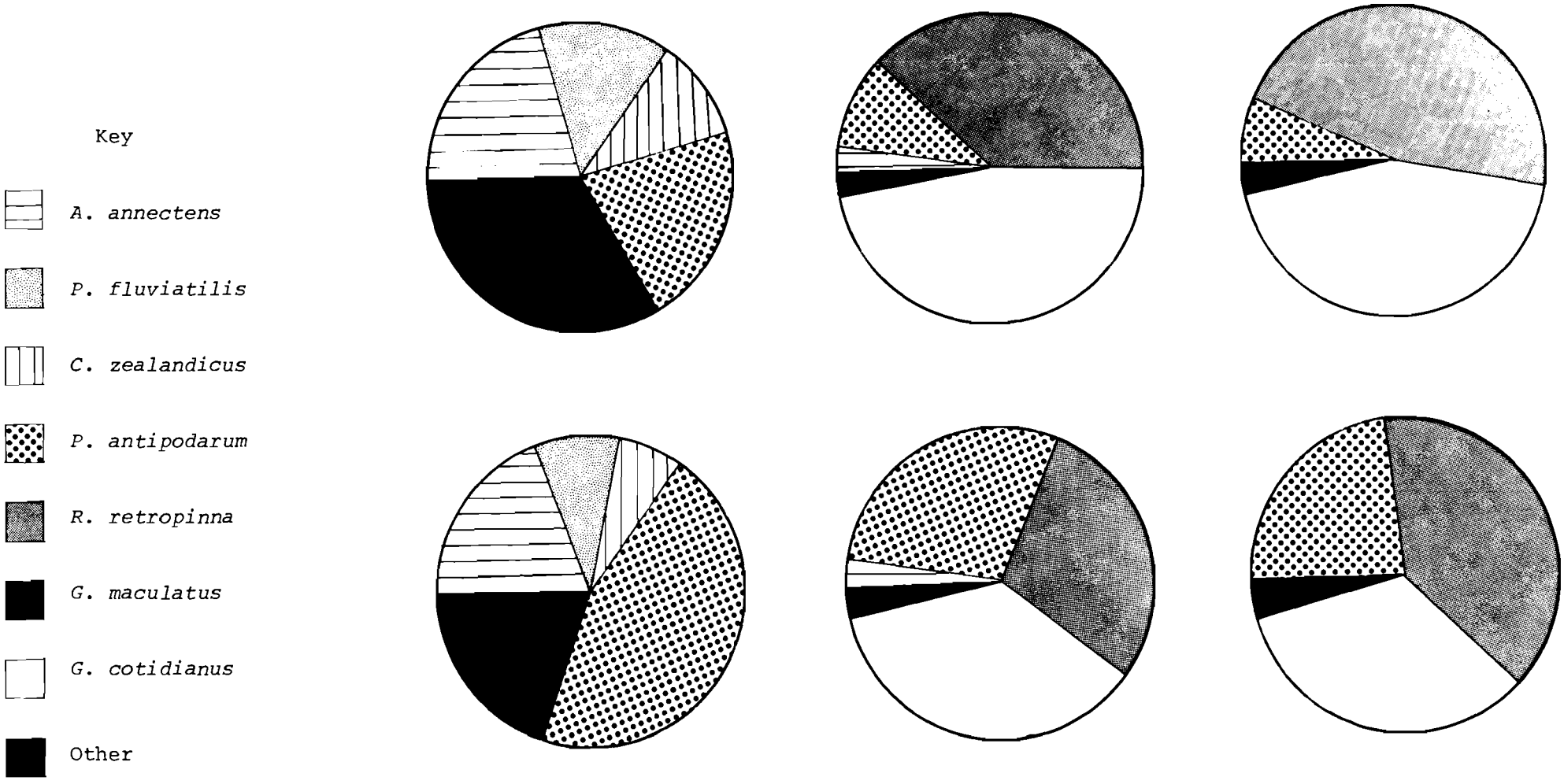


Fig. 5. The percentage contribution of food organisms in spring, expressed calorifically (upper row) and as dry weight (bottom row) for ≤40 cm eels (lefthand column), 40.1-50 cm eels (centre column) and >50.1 cm eels (righthand column).

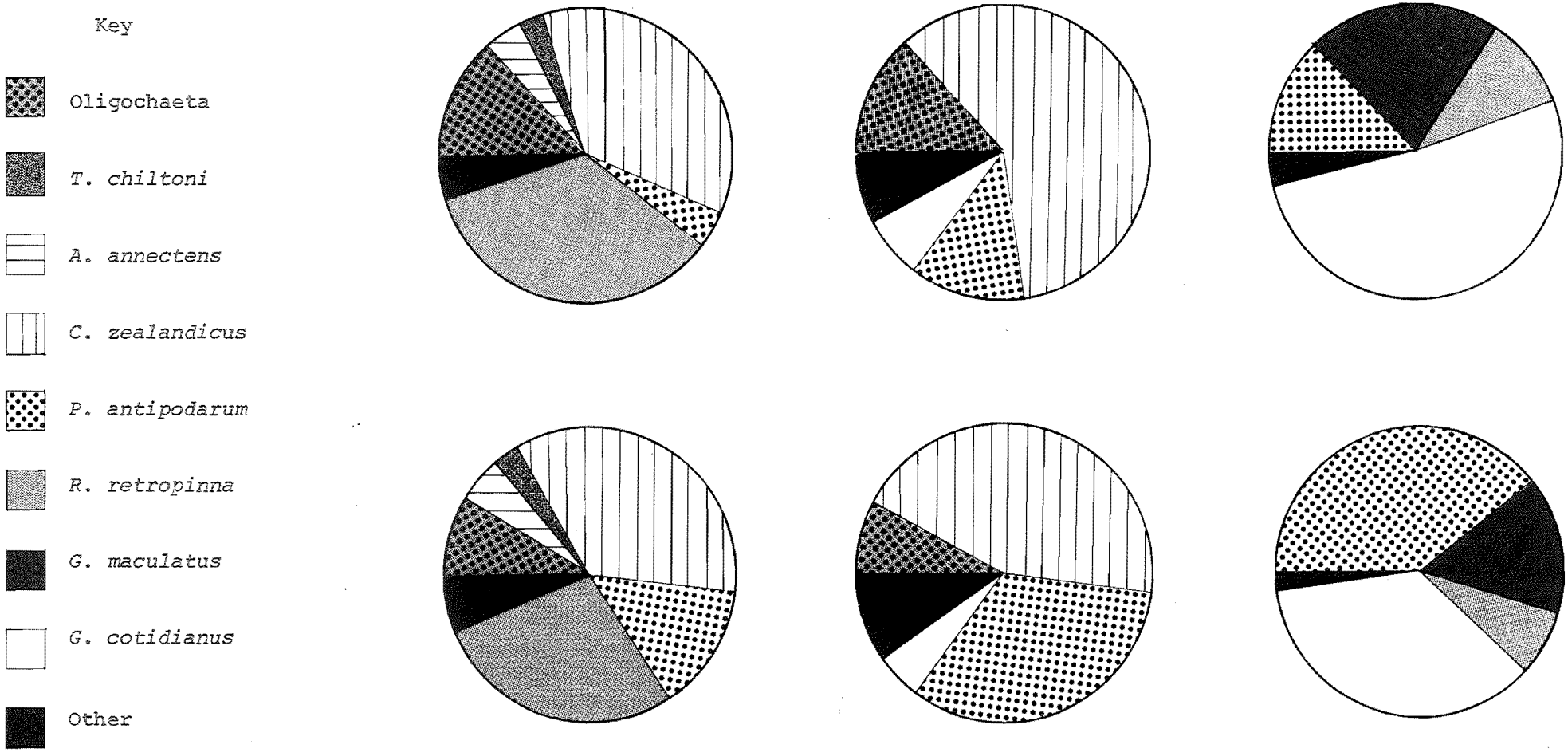


Fig. 6. The percentage contribution of food organisms in summer, expressed calorifically (upper row) and as dry weight (bottom row) for ⩽40 cm eels (lefthand column), 40.1-50 cm eels (centre column) and >50.1 cm eels (righthand column).

contributes only 8.3% calorifically. The large drop from spring to summer in fish as prey organisms for this size class of eels is probably due to the great increase in availability of *C. zealandicus*. Large numbers of 4th instar larvae, which often leave their burrows (Forsyth, 1971), become readily available as do pupae and newly emerged adults. Swarms of chironomid adults are characteristic of late summer at Lake Ellesmere and at times become extremely dense. On hot days hundreds of pillars of adults appear like smoke over the lake edge. The density of larvae and pupae prior to this emergence must also be high. In contrast, *C. zealandicus* makes a minimal contribution to the food of the >50.1 cm size class which remains predominantly piscivorous.

In autumn (Fig. 7) there are still sufficient numbers of *C. zealandicus* larvae for them to be important food items and they contribute 21.3% of the diet (in calorific terms) for eels ⩽40 cm. *A. annectens* remains an important food item with 12.6%, and *T. chiltoni* increases in importance to 12.5%. *G. cotidianus* is most important calorifically with 36.5% but 63% of the calorific input is still from invertebrates. *C. zealandicus* is almost as important to the 40.1-50 cm size class as it was in summer, contributing 30.4% calorifically and is surpassed only by *G. cotidianus* with 35%. *T. chiltoni* becomes very important with 20.3%. Unfortunately no information is available on the life history of *T. chiltoni* but examination of the length/dry weight data suggests that this species breeds in early spring. It is possible that with the onset of cooler water in autumn the previous season's adults become less active and more easily caught, but until further work is carried out on this species this suggestion must remain speculative.

Invertebrates, as in summer, contribute most to the diet of 40.1-50 cm size eels. Eels longer than 50.1 cm remain highly piscivorous with *G. cotidianus* (45%), *R. retropinna* (40.2%), *G. maculatus* (4.8%) and *Carassius carassius auratus* (3.5%) providing 94% of the calorific input.

When seasonal figures are pooled for each size class (Fig. 8), comparisons can be made between the diet of each size class on an annual basis. Invertebrates figure prominently in the diet of the ⩽40 cm size class, their total calorific contribution being about 70%. Fish occur in small numbers but because of

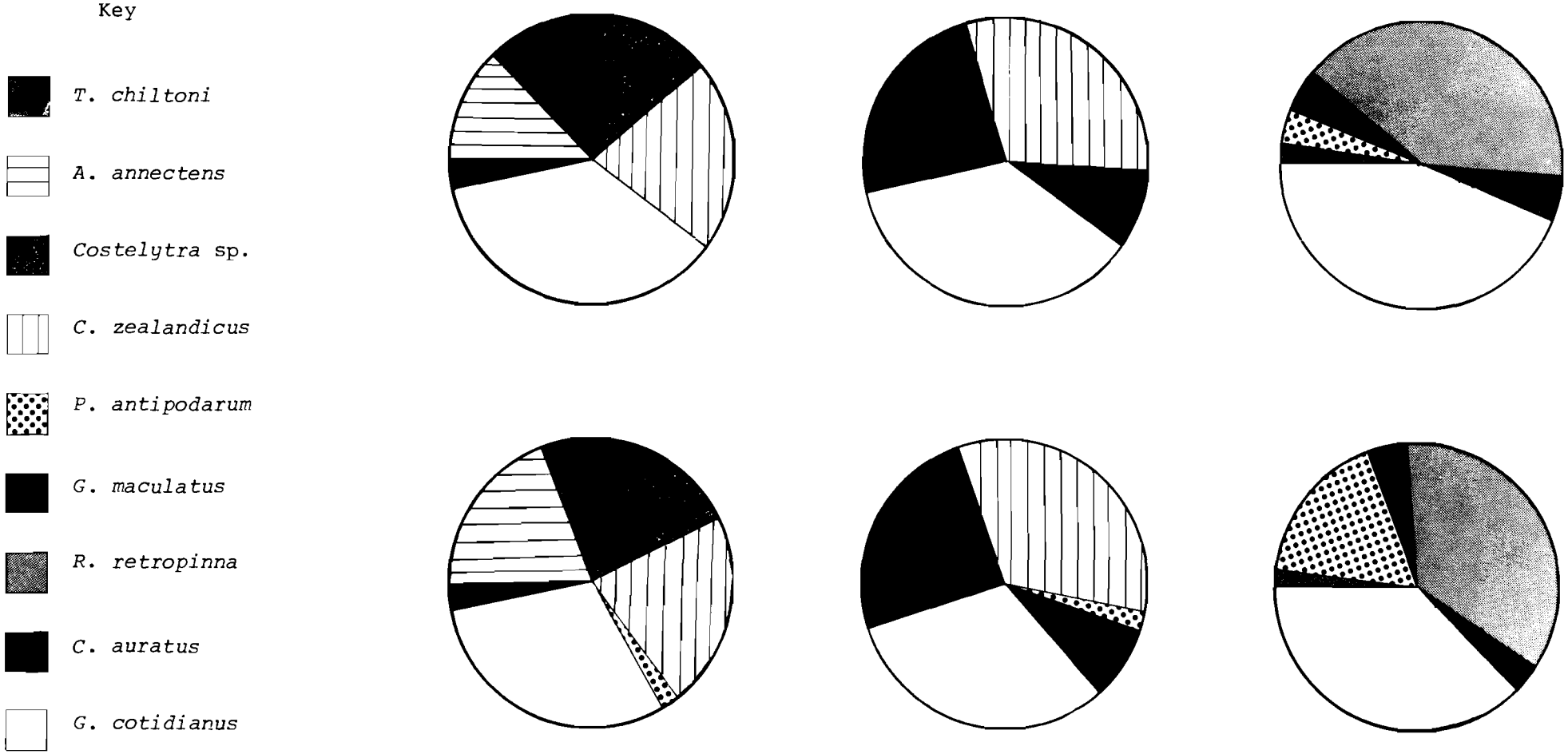


Fig. 7. The percentage contribution of food organisms in autumn, expressed calorifically (upper row) and as dry weight (bottom row) for ≤40 cm eels (lefthand column), 40.1-50 cm eels (centre column) and >50.1 cm eels (righthand column).

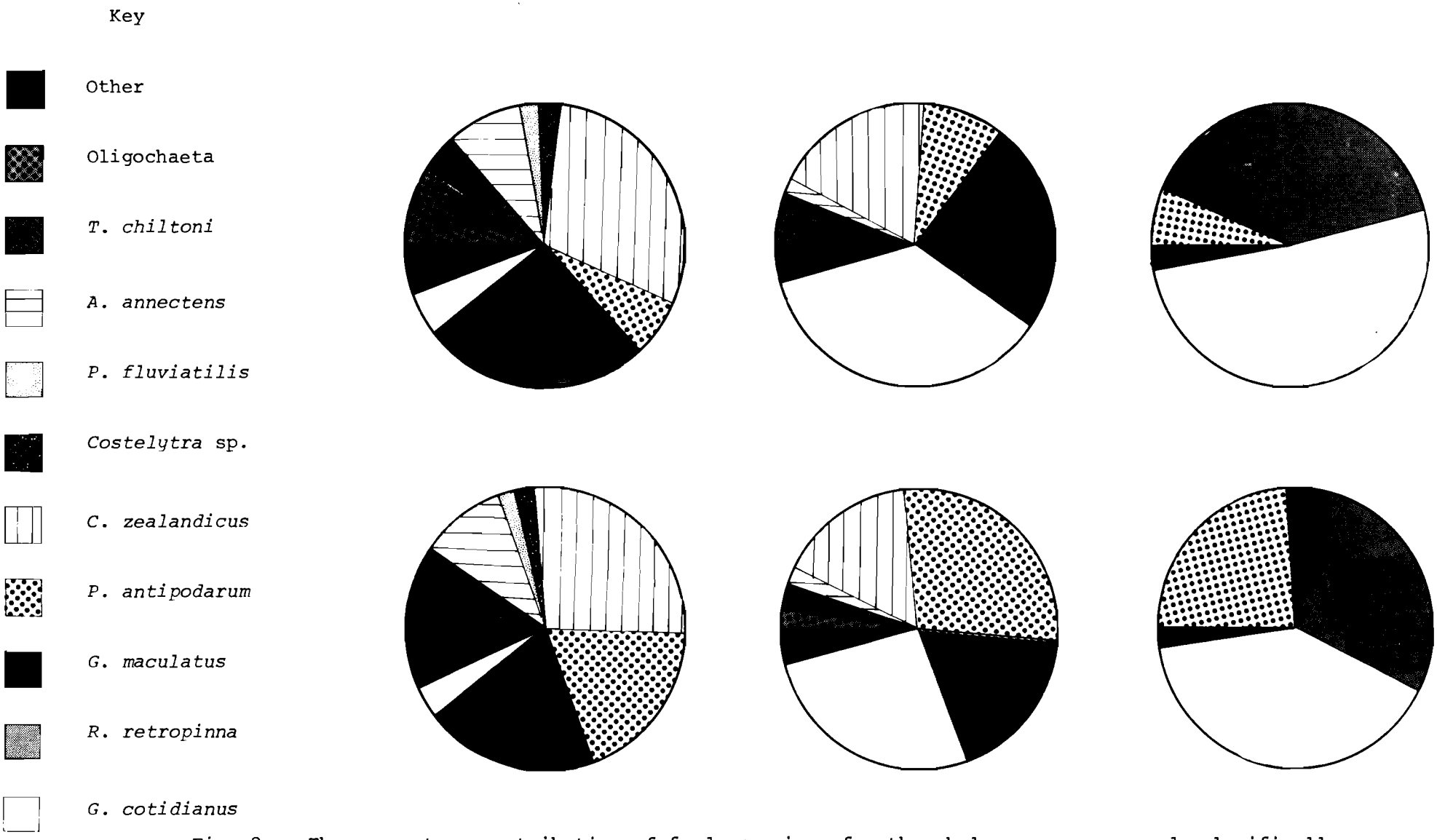


Fig. 8. The percentage contribution of food organisms for the whole year, expressed calorifically (upper row) and as dry weight (bottom row) for ≤40 cm eels (lefthand column), 40.1-50 cm eels (centre column) and >50.1 cm eels (righthand column).

their size still make a large contribution. The smallest eel in which a fish was found was 37 cm, so apparently only the larger eels in the size class consume such large prey. The 40.1-50 cm eels are more piscivorous, with 60% of their calorific input coming from fish. *C. zealandicus* with 18.3% was the most important invertebrate followed by *P. antipodarum* (9.3%). If dry weights only are considered, *P. antipodarum* is the most important food item. The >50.1 size class are almost entirely piscivorous, with 90% of the calorific input supplied by *G. cotidianus* (50.7%), *R. retropinna* (33.7%) and *G. maculatus* (5.5%). *P. antipodarum* contributed 6.5%.

Pooled inputs for all eels (Fig. 9) demonstrates once more the huge importance of fish to the eel diet. However, pooling the data masks the importance of invertebrates to the two smaller size classes in each season and gives a misleading impression of the importance of fish to the population as a whole. Subsequent studies on eels should keep the size classes and seasons separate to avoid such distortion. Comparison of dry weights and calorific values demonstrates almost without exception differences in expressing the relative importance of food items in the diet. These differences are particularly marked with organisms of low calorific value such as *P. antipodarum* and *A. annectens*. Although calorific values appear to be the more accurate method of expressing the importance of prey, it must be remembered that relative assimilation efficiency could alter the rankings. Some experiments on assimilation efficiency were carried out and the results are presented in Chapter 3.

Overseas publications on feeding in the eel are mainly from Europe, probably partly because of the importance of the fishery there. These publications, on *Anguilla anguilla*, present somewhat contradictory results due in part to real differences but due also to apparently faulty analysis of available data. Hartley (1940) examined 27 eels from East Anglia and concluded (from somewhat scanty data) that these eels were actively piscivorous, and changed their food as they grew. Small eels fed primarily on molluscs, insects and planktonic crustaceans and as they got bigger changed to fish, bottom living crustaceans and perhaps plants! In general outline this conclusion is very similar to the results of the present study. Frost (1946) examined the stomachs of 180 eels of various sizes from the Windermere catch-

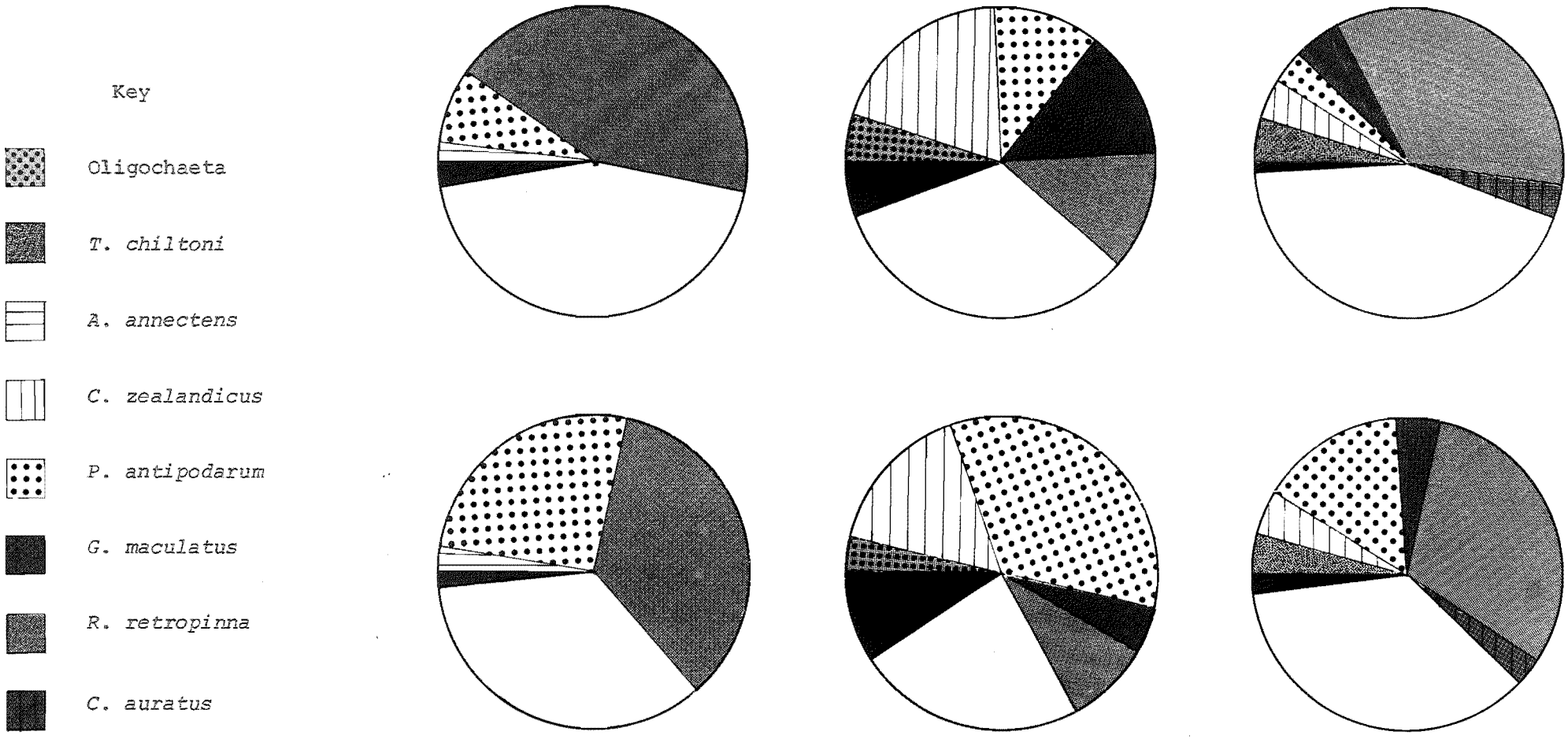


Fig. 9. The percentage contribution of food organisms to the diet of all eels, expressed calorifically (upper row) and as dry weight (bottom row) for spring eels (lefthand column), summer eels (centre column) and autumn eels (righthand column).

ment and found that molluscs were the most important food item. Fish were found in very few stomachs. Jones and Evans (1960) found that the food of eels from mountain streams in North Wales consisted primarily of insects and crustaceans. Fish were of negligible importance. Draganik (1962) studied eels from the Polish Masurian lakes and found fish to be the most important food item. He also found that eels did not feed during the winter months and there was no change in diet with increasing eel size. Interestingly, Draganik found differences in food intake depending upon the shape of the eel head. Fish were found in 64.2% of the so-called broadheaded eels and only 32.4% of the sharp-nosed eels. Differences in the shape of snouts from eels in Lake Ellesmere were also noted but no measurements were taken. Experiments, described in Chapter 3, involving the force-feeding of eels with fish did support Draganik to some extent. Broadheaded eels were much easier to force-feed with *G. cotidianus* due primarily to a larger oesophagus than the narrownose eels. Cragg-Hine (1964 and 1964, quoted in Sinha and Jones, 1975) examined eels from the Nene watershed of East Anglia. In his study fish comprised 75% of the volume of food eaten; amphipods and isopods were also important. Rogers (1964) examined the stomachs of 250 eels from the Cottage River in Ireland and concluded that various invertebrates provided the bulk of the food. Fish were of minor importance. Sinha and Jones (1967b) examined stomachs of about 5000 eels from rivers in Wales. Data for volume of prey species (in addition to number and percentage occurrence) are presented only for the River Wen and the River Dwyfach. In the River Wen, fish comprised 69.5% by volume of the diet and only 4.1% by number and 5.5% by percentage occurrence. In the River Dwyfach fish comprised 33% by volume, 2.3% by number and 5.2% by percentage occurrence. Despite the overwhelming importance of fish by volume, in these river systems at least, the authors conclude that "fish did not constitute a major portion of the eel diet." This conclusion is probably based upon the low total number or percentage occurrence contribution of fish to the diet and highlights the need for a uniform approach to such studies. Sinha and Jones found fish in eels as small as 22.8 cm, which is much smaller than the smallest eel to have eaten fish in the present study (37 cm). Fullness index data is not tested for significance but does

suggest that feeding is restricted from April to September. The authors conclude that there is no significant change in diet with increasing size but point out that few eels over 50 cm were caught and therefore this cannot be confirmed. Deelder (1971), in a comprehensive review of relevant literature, has little to say about eel diet but concludes that they are "fully catholic with regard to animal food provided it is alive or extremely fresh." Moriarty (1972), in a study of eels in the lakes of the Corrib system (Ireland), presents data for different eel size classes. Eels of less than 50 cm fed largely on invertebrates but above this size fish-eating became more important. Eels of 60 cm or longer fed almost exclusively on fish. Shafi and Maitland (1972) examined 22 eel stomachs from a small lake in Scotland. Their results, while hardly significant from such a small sample size, show fish to be the most important diet item. Biro (1974), in an extensive study of eels from Masurian lakes, found differences between the food of eels from littoral and open water areas. As Lake Ellesmere is "all littoral" his open water results need not concern us here for comparative purposes. In the littoral, Biro found isopods, amphipods and *Neomysis* (mysids) to be the most important food items. These results were based on numerical occurrence data only. Moore and Moore (1976) studied the diet of several estuarine fish, including *A. anguilla*. Their results showed an almost complete absence of fish from the eel's diet. The most important food items were the shrimp, *Crangon vulgaris*, and the mysid, *Neomysis integer*. Moore and Moore conclude that the smallest prey regularly ingested was around 1.0-1.7 cm which is somewhat larger than the average size of prey species found in the present study.

Little work on feeding has been done on the American eel, *Anguilla rostrata*. Godfrey (1957) examined 382 eels from four New Brunswick streams. He concludes that eels are important fish predators. Ogden (1970) found insects, oligochaetes, bivalves and crustaceans to be major diet items. Wenner (1972) and Wenner and Musick (1975) examined stomach contents of 336 eels from brackish water regions of rivers in the Lower Chesapeake Bay. Contents were sorted, identified to species where possible, counted and the volume estimated by water displacement. Crustaceans, bivalves and polychaetes made up the greatest part

of the diet but fish occurred only rarely.

Some work has been done in New Zealand on the feeding of the two New Zealand freshwater eels *Anguilla dieffenbachi* and *Anguilla australis schmidtii*. The earliest work, by Cairns (1942), involved the examination of nearly 10 000 eels of which 6 092 had empty guts. Cairns did not measure the prey organisms but did express their importance both as number of occurrences and number of individuals. Cairns divided his samples into size classes, but unfortunately pooled most of his data which reduces its usefulness. Long-finned and short-finned eels were pooled for his ⩽40 cm sample, but his 40-75 cm short-finned eel size class fed primarily on freshwater snails, small dipteran larvae (chironomids ?) and crustaceans. Because no relative sizes of prey organisms are given in his study, it is impossible to compare the relative importance of food items between his study and the present one except to conclude that in both studies freshwater snails were important items. Burnet (1952) demonstrates the importance of fish to eel diet in weedy rivers. He concludes that fish are easier to approach and capture in a weedy situation than in an open shingle stream. In shingle streams Trichoptera and Ephemeroptera larvae were most important. Hopkins (1965) studied 13 eel stomachs from Wellington streams and concluded from this small sample that the major food item was *Deleatidium* larvae. In a later study, Burnet (1969a) examined eel food preferences in the South Branch of the Waimakariri River and found that Polycentropid caddises were the most important item followed by *Physastra, Pycnocentria* sp. and *Deleatidium*. Fish were not of importance. Hopkins (1970), in a more comprehensive study than his earlier one, examined stomachs of both New Zealand species of eel from a brown trout nursery stream and found little difference between them. Cadwallader (1975) examined the feeding relationships of galaxiids, bullies, eels and trout in a New Zealand river but unfortunately combined his samples from the stomachs of the two species of eel. Both species fed on insect larvae, but as only 11 *A. a. schmidtii* were included, the relative importance of its diet items is masked by the prey species from the 54 *A. dieffenbachi* sampled. Cadwallader compared the diet of each of the species concerned and found significant overlap between *Salmo trutta* and the *Anguilla* spp. Only *G. breviceps* fed on *P. antipodarum* which, in view of the importance of this

species as eel food in Lake Ellesmere, is surprising.

A comprehensive literature review of practically all the known information about all species of freshwater eel is given by Tesch (1973) in his comprehensive work "Der Aal".

Because of differences in the type of analysis of food data of the eels studied it is difficult to draw any overall conclusion from the literature. It seems that eels will feed on almost any organism and the relative importance of any food item varies from area to area. Fish are of great importance to the diet, and those studies that do not incorporate a dry weight or volume measure of prey organisms grossly underestimate their importance. In this study eels appear to be opportunistic feeders; when a food source is abundant they will utilise it to the fullest. In summer some eels contained only *C. zealandicus* larvae while throughout the year many eels contained only *Potamopyrgus*. In one case an eel had eaten 999 specimens of this snail! (and nothing else!).

In none of the studies was any attempt made to estimate the pre-ingested weight of prey organisms. This lack tends to bias the results in favour of smaller organisms because in general small prey do not have to be fragmented to pass through the pyloric sphincter. Large items such as fish have to be considerably digested before gastric evacuation can be effected.

Hartley (1940), Cairns (1942), Burnet (1969) and Moriarty (1972), found, as in this study, that eels change their diet as they grow. They feed primarily upon invertebrates while small and become more piscivorous as they grow. In Lake Ellesmere, eels $\leqslant$40 cm depend largely upon invertebrates, and become increasingly piscivorous until they reach 50 cm, after which they are almost entirely piscivorous. Draganik (1962) and Sinha and Jones (1967b) found no change in the diet as eels grow. The other studies did not attempt such an analysis. Cairns (1942) believed that eels of $\leqslant$40 cm have a gape too small to capture, hold or swallow large food organisms. The gape does not have to be particularly large to allow fish to be swallowed as one fish of $\leqslant$40 cm had ingested a *G. cotidianus* of 4 cm (reconstructed length). Frost (1946) showed, by simple force-feeding experiments, that a 40 cm eel could swallow 5 cm trout fingerlings. The relative lack of fish in the diet of $\leqslant$40 cm eels must be due to behavioural rather than physical reasons. Presumably even

if there were physical restrictions on the size of fish that could be ingested, this would not prevent small eels ingesting small fish.

Burnet (1952) found that eels were more successful at feeding on trout in weedy streams than open streams. Lake Ellesmere is always extremely turbid and eels feed primarily at night so the success of eels in feeding upon fish may be due to their ability to closely approach prey without being seen. The great importance of fish as food for the larger size classes of eel is somewhat surprising in view of their apparent ineptness in catching fish. During feeding experiments eels occasionally seemed unaware of fish until they touched them. When an injured *G. cotidianus* was placed in their tanks, the eels initiated apparently random search behaviour with frequent movements of the head from side to side. It appeared that fish were tracked down by olfaction as the course of the fleeing fish was often followed closely. On occasions while apparently following a scent eels passed within millimetres of the prey they were pursuing with no apparent awareness of its presence. When prey were reached only one attack out of four was successful. In view of this lack of success in catching injured prey in small confines it seems surprising that so many fish appear as prey.

The clarity of the water may have enabled the prey to see and avoid the approaching eel. Von Fritsch (1941) and Mohr (1969), (cited in Deelder (1970)), have shown that an imitation worm or other bait dangled in front of eels evinced little interest. Any object which had been placed for a time in a tin of worms caused immediate excitement showing that chemo-sensory perception plays an important role in feeding. Hara (1971) states that the olfactory organ in eels is well developed. During the present study a one-eyed eel from the Selwyn River appeared to be in good condition, and no scarring was present around the missing eye, so its absence was probably due to a genetic or embryological deformity. If vision played an important role in eel feeding this eel could be expected to have been in poor condition.

Cadwallader (1972) has shown that eels possess taste buds over the external surfaces of the head. These may be useful in hunting. In the present study eels frequently swam over motionless *G. cotidianus* and in most cases any contact between

the undersurface of the jaw and the prey was followed by rapid backward movement of the eel and a subsequent ingestion attempt. Observation showed that prey was normally ingested with a powerful inrush of water brought about by vigorous opercular movements. Observations of a pet eel suggest that eels may become more proficient at hunting fish, so a positive feedback system may be in progress. Eels that feed on fish become more successful in feeding on fish. As there seems to be no physical limitation to prevent small eels feeding on fish it may be that small eels are just inexperienced.

Capture of the other major prey species would not seem to present any great problems as most are relatively sedentary. *T. chiltoni* would appear to be the most difficult to capture as they possess a violent sideways escape reflex which may be pressure induced. Slow eel approach may not create large enough pressure waves to trigger the reflex.

No previous studies on the eel have attempted to evaluate feeding success by recreating the pre-ingested length of prey organisms and determining their pre-ingested weight and calorific value. This lack is unfortunate as all other methods suffer because they deal only with already digested food items. This study has shown that the relative importance of *P. antipodarum* is overemphasised by all methods except calorific value. This criticism is in addition to the observation that numerical occurrence overemphasises small items and the occurrence method overemphasises infrequent items of diet.

Unfortunately there is as yet no standardised method for analysing fish diets. If all fish studies were carried out using one method, where possible, comparison of analyses between habitats and species would be made much simpler. Results from this study suggest that calorific value analysis shows which food items are of most value to a fish species. Unfortunately it is also the method requiring the most time.

## SUMMARY

Eels in Lake Ellesmere are most active in spring, as revealed by catch rate data, and activity drops through summer and autumn. Activity is minimal during the winter months. Feeding appears to take place from 2100-0600 h and fullness indices increase over this period. Analysis of 487 eel stomachs shows that the relative importance of food items in the diet changes with method of analysis, season and size class of eel. The condition factor of fish changes with season from a low in winter to a high in autumn. Comparisons of different methods of food analysis show that all have some faults. Calorific value analysis appears to produce the best results in determining relative importance of food items, but predicted dry weight gives useful information for eels eating large food items. Actual dry weight is useful for fish eating small food items. Numerical occurrence and percentage occurrence are not as accurate but are still useful. Eels $\leq$40 cm feed primarily upon invertebrates, 40.1-50 cm size classes feed predominantly upon fish but invertebrates are also important. Eels larger than 50.1 cm are almost entirely piscivorous.

# CHAPTER TWO. AGE AND GROWTH

## INTRODUCTION

If an energetics approach is to have much relevance in an ecological study of fish, some indication of growth rates must be obtained so that the amount of energy used in growth can be determined. In general, there are four ways of doing this:

1) Analysis of length frequency distributions.
2) Mark and recapture methods.
3) Direct observation of known-age fish.
4) Interpretation of the growth zones or checks that appear in the hard parts of fish (such as scales, vertebrae, opercula and otoliths). Usually there is one check per year and these checks may be counted.

Analysis of length frequency distributions is of little use in the study of eel populations as the growth rates are slow and the eels long lived which causes an extensive overlap in size between age classes (Deelder, 1970, Moriarty, 1972). Mark and recapture techniques could have been feasible but expense ruled out the use of any easily recognisable tags (such as Floy tags) and it seemed unlikely that recapture rates would be high enough for any useful information to be obtained. Direct observation of known age fish was not possible as no fish of known age were available. Interpretation of growth checks in the hard parts, therefore, appeared to be the best method and otolith analysis was adopted for this reason.

Otoliths can be used for ageing fish because checks in growth cause changes in the chemical composition of the otolith (Liew, 1974). The zones with this different chemical composition have different optical properties from the rest of the otolith. When viewed under reflected light these zones appear as narrow black transparent zones alternating with wide opaque areas. Under transmitted light the opaque zones appear dark and the dark transparent zones become light transparent. Frost (1945) and Sinha and Jones (1967a) have confirmed that the wide opaque zones represent summer growth and the black zones the winter checks.

Many age and growth studies have been undertaken on the European eel *Anguilla anguilla* using otoliths to age the fish.

Ehrenbaum and Marukawa (1913) validated the use of otolith annual rings, and also showed that scales were of little use in age determination. Sinha and Jones (1967a) listed the most important subsequent studies. Recently Wiedemann Smith (1968), Champ (1968), Tesch (1970), Moriarty (1972), Benech (1975), Deelder (1976), Moriarty and Steinmetz (1976) and Parsons *et al.* (1977) have also studied the age of the eel using otoliths. Some studies on wild populations of *A. japonica* have been published in Japanese but little information is available in English. Balon (1975) studied the African eel, *A. nebulosa labiata* in Lake Kariba and determined growth rates by back calculation of otoliths. Age determinations using the otoliths of the Indian eel, *A. nebulosa* have been made by Pantulu and Singh (1962). Ogden (1970), Gray and Andrews (1971), Hurley and Donal (1972) and Liew (1974) used otoliths to age the American eel, *A. rostrata*. Smith and Saunders (1955) used scales to age eels but found that results were variable.

A number of studies have been made of the age and growth of the New Zealand eels, *A. australis schmidtii* and *A. dieffenbachi*. MacFarlane (1936) determined eel ages by using scales and otoliths. Cairns (1941) used otoliths for ageing but concluded that scales were also satisfactory. Burnet (1969) made a detailed study of age and growth in three separate streams using otoliths and tag returns. Todd (1974) made age determinations using both otoliths and scales and concluded, contrary to MacFarlane and Cairns, that scales are not suitable for age determination.

METHODS

Early attempts to grind otoliths with carborundum and view them under reflected light were not successful. The curved nature of the otolith caused the outside rings to be lost when grinding was taken to a point which provided a satisfactorily thin otolith. Attempts to oxidise proteinaceous material between growth zones using potassium permanganate solution were not successful, nor were attempts to bring about differential staining of growth zones using methyl violet B, a method used by Albrechtsen (1968). Burning otoliths on a scalpel blade over a bunsen flame, as outlined by Christensen (1964), appeared to be the most promising method. Initially otoliths were split in half across their short axis and each half burned. The break was often ragged and, even when the otolith was viewed under immersion oil, proved difficult to read. Grinding the flat edge of the break, and then burning, did not improve readability as the otolith often splintered. The method outlined by Moriarty (1972) proved the most successful. Moriarty does not break the otoliths before burning but lets them do so of their own accord while in the bunsen flame. Usually an otolith splits across the short axis to give two nearly equal pieces. Otoliths that do not break are placed convex side upwards and gentle pressure exerted with a scalpel blade across the short axis. Each otolith was burned for between 30 and 60 seconds depending on its size.

To view such otoliths satisfactorily they must be embedded in a suitable mounting medium so that the burnt surface remains horizontal. Keeping the halves horizontal initially presented problems. The heat from the microscope lights, in conjunction with the acidic nature of most suitable refractive media, softened plasticene, gutta percha, and a plastibond resin which were employed for the purpose. The most satisfactory material was a silicone rubber compound which was squeezed over a glass microscope slide and left for a few minutes to "skin". Otolith halves were picked up using a fine needle and a small drop of silicone rubber. The four halves from each fish were inserted face upwards in the silicone rubber and manipulated under a low power stereo microscope until the faces were horizontal. The rubber compound set solid in 12 hours and was impervious to heat

or immersion oil. Otoliths from 336 eels were mounted in this manner with otoliths from five eels in groups on each slide.

Otolith measurement

Each otolith was viewed under a stereo microscope at x 40 magnification using reflected light with immersion oil providing the refractive medium. Summer growth zones appeared white and winter checks black. For the purpose of back calculation an eyepiece micrometer or a camera lucida could not be used satisfactorily as the number of false rings and the extremely slow growth rate made discrimination difficult. Otoliths were therefore photographed through a binocular microscope at approximately x 20 magnification using an Asahi Pentax K2 camera body and a Pentax microscope adapter. The light source was a National PE 2810 flash unit held 2.5 cm from the slide. To eliminate possible reflections, each otolith was viewed with an oblique light source and the slide rotated until reflections disappeared. The flash was then oriented in the same direction as the light source. The film used was Agfapan 25 uprated to approximately 200 a.s.a. by developing for 25 minutes in Rodinal diluted 25 to 1 at 22°C. This development procedure had the desired effect of greatly increasing contrast between the growth zones. Photographs were printed on Agfa A4 size document paper, two to a sheet.

Initially all otolith photographs were measured, using dividers, from the centre of the glass eel nucleus to the outside of the otolith, which is in keeping with the previous back calculation practice for eels (Pantulu and Singh, 1962, Liew, 1974, Balon, 1975). This practice assumes, perhaps incorrectly, that the same relationship between otolith growth and eel growth pertains in the leptocephalus and glass eel as does in the elver. This assumption is difficult to verify - especially when it is considered that the leptocephalus shrinks during metamorphosis into a glass eel. For this reason the seawater section of growth was not used in measuring growth in freshwater. Jellyman (1977, *pers. comm.*) has established that, upon arrival in freshwater, glass eel have (in burnt otoliths), a black nucleus, a wide white zone of summer growth and a black narrow winter ring. Therefore, measurements were taken from this first black winter ring to the outside of the otolith. To determine the relation-

ship between otolith growth and eel growth, total eel length for 205 eels was regressed on otolith length measured in the manner described above. This regression intercepted the length axis so the back calculation took the form:

$$\ell_n - c = (s_n/S)(L - c)$$

where $\ell_n$ = length of fish when annulus 'n' was formed
$L$ = length of fish at time otolith sample was obtained
$s_n$ = radius of annulus 'n' (at length '$\ell_n$')
$S$ = total otolith radius
$c$ = intercept on the length axis.

Liew (1974) in his back calculation study, incorrectly perhaps, assumed direct proportionality between otolith growth and eel growth and did not take a constant into account. His back calculation results are therefore not entirely accurate.

Each growth ring radius was measured with a pair of dividers from the point of greatest growth on any particular annulus to the outside of the first black winter ring. The greatest total overall radius of each otolith was also measured. In some cases annuli became unreadable towards the perimeter because of slow growth rates but in these cases all legible rings were measured for the purpose of back calculation. Each otolith was assigned a readability index as shown below.

1 - No rings readable
2 - Some inside rings readable
3 - All rings visible with difficulty
4 - All rings reasonably readable
5 - All rings clearly readable

Some otoliths grew in an asymmetrical manner with the point of greatest growth on any given ring tracing a C shape as the otolith grew (see Plate 2). On such otoliths it was considered that a straight line measurement from the point of greatest growth of the whole otolith to the outside of the glass eel winter ring would proportionately decrease as the otolith curved. In these cases the line of greatest growth was fitted to the photograph by eye and intervals between annuli measured along this line and summed to give each successive radius. Comparison between otoliths measured in this way and those read by measuring the radius directly revealed such minimal differences that all curved otoliths were read subsequently by measuring the radius directly. Some otoliths proved difficult to read due to slow

Plate 2. A curved otolith of readability class 2 from an age class 27 eel. x200 magnification.

growth rates and the resultant crowding of annuli. Not utilising such otoliths in a growth study would tend to bias the apparent population growth rate in favour of faster rates. In an attempt to determine the effect these otoliths make on the growth rate of the population, separate growth curves were obtained for otoliths with readability indices of 2, 3, 4 and 5 and compared with each other and with the growth curve obtained from all otoliths. No attempts were made to establish whether the outside edge of the otolith represented a winter or summer growth zone as the edges were inevitably badly charred. All ages were taken, therefore, to the last positively identified winter zone and total otolith radius was always taken to the extreme outer edge of the otolith. Use of this procedure probably led to underestimating age by up to one year, but gave better standardisation of readings.

All growth curves were fitted by computer from the back calculation data. A programme was also designed to find periods of rapid or slow growth amongst known-age fish. This calculation was done by comparing the actual back calculated annual growth for each fish with its expected annual growth determined for its age class from the back calculated growth rate. These increments were summed for each year class and the mean increment for any year class compared with the expected increment.

If back calculation can be applied to a study it increases the available information markedly. In the present study back calculation boosts the number of age-length pairs from 325 to nearly 4000. Growth rates of undifferentiated (for which sex could not be determined) and female fish were compared to determine any sexual differences in growth rate. Growth rates obtained were fitted with the von Bertalanffy growth equation.

To enable growth rates to be expressed in energy terms, the calorific value of eel flesh was needed. Calorific values of 11 eels of different lengths were determined. The fish were taken in autumn (April) when they exhibit their greatest calorific value (Hopkirk *et al.*, 1975). Each fish was measured to the nearest 1 mm on a V-shaped measuring board, oven dried at 70°C to a constant weight and ground in a Waring commercial blender. Calorific determinations were than made with a Gallenkamp oxygen bomb calorimeter and the total length/calorific value

regression line fitted by computer. Age/calorific value curves were then fitted to give the average increase in calorific value for each successive age class.

The results of 1597 age/length pairs for female fish and 2353 pairs for undifferentiated fish presented in this study are based upon the assumption that Lake Ellesmere eels lay down one winter ring a year. This assumption has certainly been shown for *A. a. schmidtii* in other regions (Todd and Jellyman, *pers. comm.*) and has long been accepted as the case for the European eel, *A. anguilla*, but Dahl (1967) and Moriarty (1975) demonstrated that it is not true for all fish. Deelder (1976) investigated this problem and concluded that densitometry was able to distinguish between false summer checks and winter checks. He also concluded that photography would probably also be satisfactory.

Moriarty and Steinmetz (1976) compared four different otolith preparation techniques; polishing and staining, burning, densitometry, and the conventional method (examination of the otolith under a binocular microscope using creosote as the refractive medium). The authors found no general agreement between the methods used and conclude that the comparability of readings of eel otoliths by different research workers may be small.

Panella (1971, 1974) has shown that daily rings are laid down in the otoliths of some marine and freshwater fish, as have Taubert and Coble (1977) for several species of freshwater fish. Low temperatures inhibited daily ring deposition but an annulus was still formed.

Liew (1974), using scanning electron microscopy on acetate replicas from ground otoliths of *A. rostrata*, was able to validate age determination and back calculation for the American eel. It appears that sudden temperature change or a low food supply may bring about a temporary check in otolith growth that can be misinterpreted as a winter check. False rings in otoliths from Lake Ellesmere eels do not usually extend completely around the otolith and it was possible to differentiate them in the photographs. Furthermore, as Lake Ellesmere is a large body of water, the extent of temperature fluctuations present in the pond in Liew's study are unlikely to be encountered. It was assumed, therefore, that otoliths from Lake Ellesmere eels could be used for back calculation.

RESULTS AND DISCUSSION

Back calculation is now a widely used tool in fisheries research. In this study, measuring otoliths from the winter ring of the glass eel, instead of the nucleus as in previous studies, removes any possible speculation over the relative growth rates of the leptocephalus, glass eel and the elver. Validation of back calculation in this study also comes from the results of the back calculations. Skr zynski (1974) gives the size of glass eels, upon their arrival in freshwater, as 6-7 cm. Age class 0 fish were calculated to be 8.82 cm long. Lengths of fish of known age at capture (determined by counting all rings) were compared with back calculated lengths for every age where there were sufficient samples for a valid comparison. Few young fish were caught and few old fish were aged sufficiently accurately, so only age classes 7 to 16 were compared in Table 26. The lengths from back calculated data give very

Table 26. Lengths of fish at different ages from back calculation compared with mean length of known age fish. Number in each sample in brackets.

| | Back calculation | | | | | |
|---|---|---|---|---|---|---|
| | All fish | | Female fish | | Known age fish | |
| Age class | length (cm) | no. | length (cm) | no. | length (cm) | no. |
| 7 | 30.4 | (248) | 31.8 | (87) | 30.6 | (3) |
| 8 | 32.2 | (240) | 33.7 | (86) | 31.5 | (3) |
| 9 | 34.0 | (228) | 35.6 | (83) | 37.0 | (6) |
| 10 | 35.6 | (216) | 37.3 | (80) | 38.3 | (8) |
| 11 | 37.1 | (199) | 38.5 | (75) | 40.5 | (8) |
| 12 | 38.4 | (180) | 39.9 | (71) | 39.7 | (10) |
| 13 | 39.6 | (156) | 41.5 | (65) | 41.2 | (17) |
| 14 | 41.1 | (129) | 42.8 | (58) | 42.8 | (12) |
| 15 | 42.3 | (106) | 43.9 | (51) | 43.7 | (14) |
| 16 | 43.7 | (82) | 45.1 | (46) | 45.1 | (10) |

similar results to the measurements of fish of known age. The greatest difference between the two results was only 3.4 cm (age class 11) and could be due to the small sample size of the known

age class involved. If growth rates of the population are faster now than they were when the fish used for back calculation were age class 11, this could also explain the small difference. It must be stressed that any growth rates for a population revealed by back calculation only describe past growth rates. While they give an indication of present growth rates, the two growth rates are not necessarily the same.

The regression equation for eel length regressed on otolith length using a computer fitted Bartletts 3 group method gave the following equation based on 183 pairs of otoliths:

| | F test for normality | Significance level |
|---|---|---|
| $L = 328.33\ \ell + 88.20$ | 1.391 | >0.05 |

where L is eel length in mm

$\ell$ is otolith radius from the first winter ring to the outside of the otolith.

The value of 88.20 was then substituted for c in the equation;

$$\ell_n - c = (s_n/S)(L - c)$$

and this back calculation equation was computer fitted to all otolith data. Because the time of capture of eels varied, a decision had to be made regarding their "birth date". The most reasonable time appeared to be the month of peak arrival of glass eels into Lake Ellesmere and, accordingly, October was chosen on the advice of P. Jellyman (*pers. comm.*). A least squares regression was fitted by computer to each growth curve obtained, but these equations were barely adequate for describing growth. The calculated regression equations are shown in Table 27. Readability class 5 was not included as the otoliths from only three fish were given this rating. No comparisons between regression lines have been attempted. According to Table 27, undifferentiated fish have the highest growth rate and female fish the lowest. These results appear to be due to the shortcomings of a least squares regression line in modelling the data, because when growth rates from back calculation are plotted graphically, female fish reveal the fastest growth rate. The similarity of results for fish of readability classes 2, 3 and 4 made it impractical to plot them on the same graph and results are presented in Tables A.22-24 instead. This result suggests that differences in readability of otoliths are not, in fact, due to the otolith itself, but are due to the preparation.

Table 27. Regression equations fitted to back calculated growth data for all fish, female fish, undifferentiated fish and readability classes 2, 3 and 4. L is fish length in mm.

| Otolith class | Equation | No. of data pairs | Correlation coefficient |
|---|---|---|---|
| All fish | L = 17.065 Age + 150.63 | 3950 | 0.905 |
| Female fish | L = 15.954 Age + 171.33 | 1597 | 0.903 |
| Undifferentiated | L = 17.949 Age + 137.61 | 2353 | 0.900 |
| Readability 2 | L = 17.913 Age + 143.637 | 2313 | 0.892 |
| Readability 3 | L = 16.698 Age + 149.318 | 2870 | 0.907 |
| Readability 4 | L = 17.201 Age + 150.862 | 946 | 0.868 |

Otolith halves from the same fish were often given different readability indices. The computer plotted growth data for each analysis are presented in Tables A.19-24.

Because of the poor fit of regression lines to the data, an alternative growth model in the form of the von Bertalanffy (1938, 1957) growth equation was applied. Parameters used in the von Bertalanffy equation were estimated graphically. Cadwallader (1975) compared the Allen least squares method for obtaining the parameters with the graphical method and concluded that the latter provided an adequate alternative. Cadwallader's procedure was followed in this study, except that graphs were fitted by computer instead of by eye. The equation, which was applied to female and undifferentiated fish only, is;

$$l_t = l_\infty(1 - e^{-k(t-t_o)}) \qquad 1.$$

where $l_t$ is the length at age t

$l_\infty$ is the average "maximum" or asymptotic length

k is a constant determining the rate of change in the length increment

t is age in years

$t_o$ is the hypothetical age when length is zero.

$l_\infty$ was calculated for female and undifferentiated fish by using the expression developed by Ford (1933) and Walford (1946).

$$l_{t+1} = l_\infty(1 - k) + klt \qquad 2.$$

Walford graphs of $l_{t+1}$ against $l_t$ were fitted by computer using Bartletts three group method. This regression gave the equations;

i) for female fish

$$l_{t+1} = 0.9082\ l_t + 52.059$$

ii) for undifferentiated fish

$$l_{t+1} = 0.9007\ l_t + 49.642$$

$l_\infty(1 - k)$ was equated to 52.059 to give $l_\infty$ for female fish and $l_\infty(1 - k)$ equated to 49.642 for undifferentiated fish. This equation gave $l_\infty$ for female fish of 567.1 mm
and $l_\infty$ for undifferentiated fish of 499.92 mm.
k and $t_o$ were calculated using the natural logarithmic form of equation 1.

$$\log_e(l_\infty - l_t) = \log_e l_\infty - k(t - t_o) \qquad 3.$$

which gives

$$\log_e(l_\infty - l_t) = \log_e l_\infty + k\ t_o - k\ t \qquad 4.$$

$\text{Log}_e(l_\infty - l_t)$ was regressed on t using Bartletts three group method to give the equations;

i) for female fish

$$\log_e(l_\infty - l_t) = -0.0797\ t + 6.0069$$

ii) for undifferentiated fish

$$\log_e(l_\infty - l_t) = -0.0963\ t + 5.9602$$

for female fish k (slope) = -0.0797
and for undifferentiated fish k is equal to -0.0963.
Values of $t_o$ were calculated by equating the y axis intercept to $\log_e l_\infty + k\ t_o$

For females $t_o = -4.18569$
and for undifferentiated fish $t_o = -2.63966$.
The von Bertalanffy equation for female fish was therefore;

$$l_t = 567.1(1 - e^{-0.0797(t + 4.18569)})$$

and for undifferentiated fish,

$$l_t = 499.9(1 - e^{-0.0963(t + 2.63966)})$$

The von Bertalanffy curves are shown in Figs 10 and 11. The theoretical curve consistently overestimates growth in female fish but only by a small amount (Fig. 10). The theoretical curve for undifferentiated fish starts at a lower growth rate than the actual growth curve but matches it by age 3 and thereafter closely parallels the population growth curve (Fig. 11). Pantulu and Singh (1962) found a good fit between growth rate of *Anguilla nebulosa* from back calculations and the von Bertalanffy curve fitted to the data. The authors conclude that the good agreement helps to confirm the validity of the use of otoliths in the estimation of age and growth. It is encouraging to find any theoretical model matching the data, however when the fit is not good the fault usually lies with the model, not with the data. Furthermore, as back calculated lengths were used by Pantulu and Singh to calculate the von Bertalanffy curve, it is not surprising that there is reasonable agreement between the two. Rasmussen (1977) fitted a von Bertalanffy curve to lengths back calculated from the otoliths of 177 yellow eels of *Anguilla anguilla*. The fit was not as good as in the present study, but gave agreement throughout the age range. Tesch (1971) believes that there is general value in fitting growth curves for descriptive purposes but that their biological interpretation still presents great difficulties. The von Bertalanffy equation was thought by its author to be justified on basic physiological principles but these principles have since been rejected (Ricker, 1958, Richards, 1959, Hemmingsen, 1960; in Tesch, 1971). Paloheimo and Dickie (1965) question the generality of asymptotic growth. In the present study, the asymptote for female fish is considerably less than the mean size of migrant females, which, according to Todd (*pers. comm.*) is 60.0 cm. The asymptote for

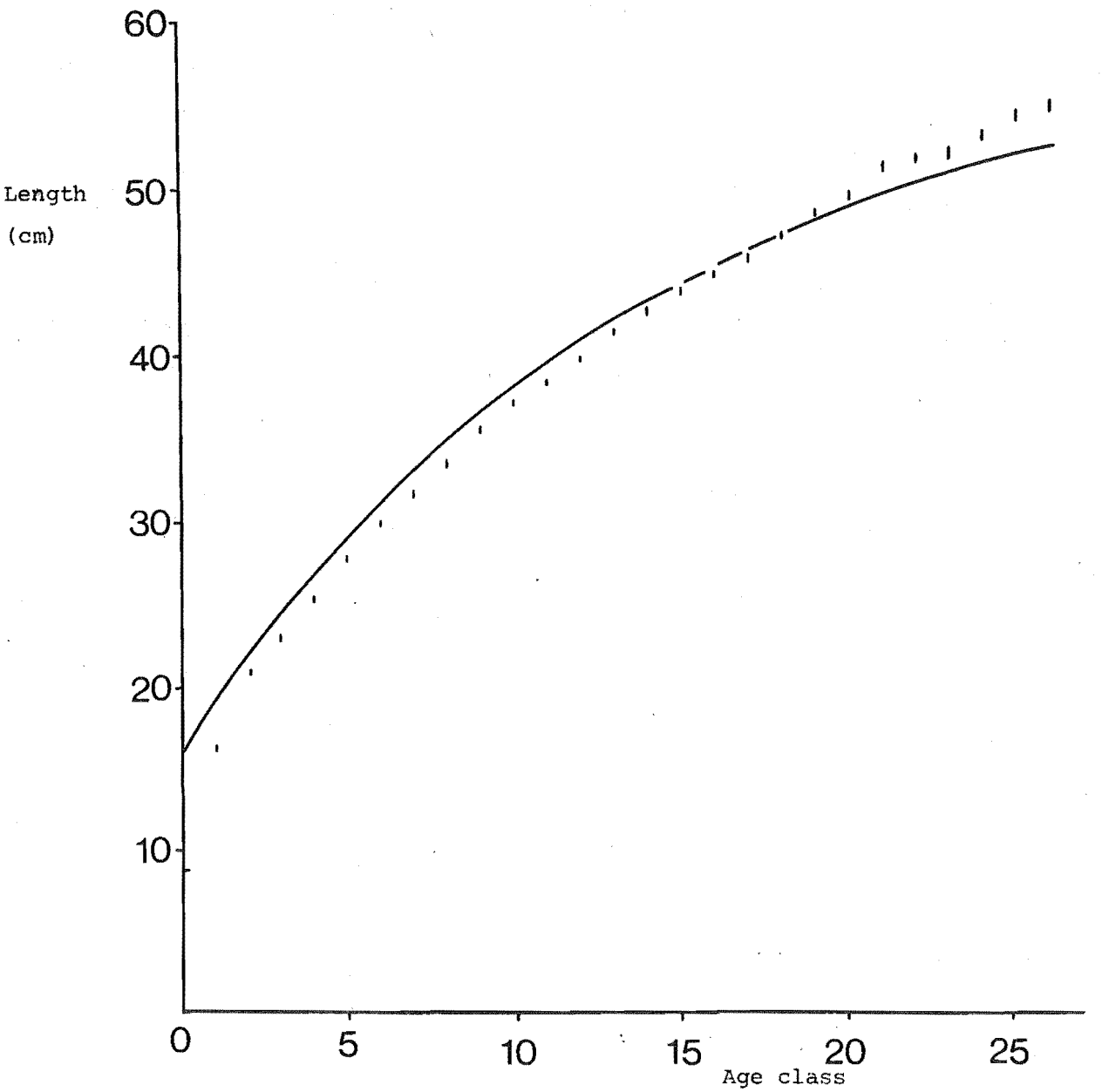


Fig. 10. The von Bertalanffy growth curve (solid line) fitted to back calculated growth data for female fish. The vertical bars show the means and their 95% confidence limits.

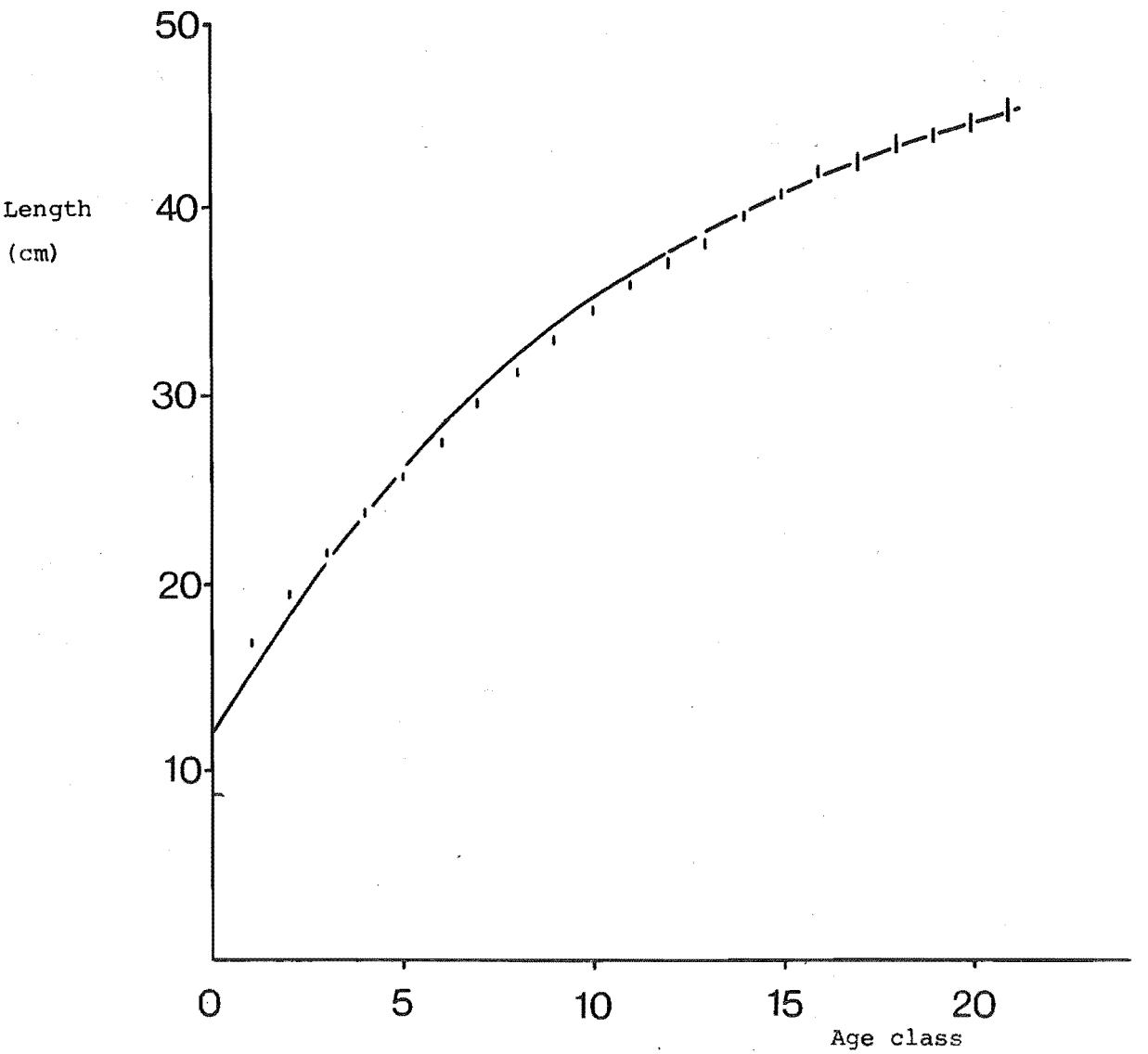


Fig. 11. The von Bertalanffy growth curve (solid line) fitted to back calculated growth data for undifferentiated fish. The vertical bars show the means and their 95% confidence limits.

undifferentiated fish lies midway between this value and the 43.9 cm length given by Todd as the mean size of migrant males. The asymptote must exist in this population as adult sexually maturing eels migrate out of the population.

The question arises, of what use is a growth model? In the present study not a lot perhaps, as the growth curves from back calculation are based on large numbers of samples and each age class is well represented. In other studies, larger size classes may not be easily captured and the von Bertalanffy equation can be used for predictive purposes. The von Bertalanffy equation also gives a "smoothed curve", thus avoiding year to year fluctuations in age class size. The main purpose behind fitting it in my study is to demonstrate that it will adequately describe eel growth in New Zealand. This fact has been demonstrated for *A. a. schmidtii*, which joins *A. nebulosa* and *A. anguilla* in having its growth adequately described by a von Bertalanffy growth curve.

Back calculated lengths were also used to compare actual growth increments in a particular year with the theoretical increments. For any given year the back calculated length of each fish was compared with its own back calculated length the previous year and the increment calculated. The mean increment for all fish extant in any given year was then determined in this manner. The theoretical growth was determined by calculating the annual increment of the age classes in question from the mean figures from the back calculated data. This approach was necessary because later year classes had a higher proportion of old fish in them, whose contribution to growth is proportionately small. Because the proportions of different age classes vary from year to year, mean and expected growth rates for any given year cannot be compared directly between years - only with each other. In general, early years contain a higher proportion of young fish than do later years because few young fish are caught in the fyke net samples. According to the von Bertalanffy equation, the smallest eel caught (23 cm) was already five years old. Table A.18 in the appendix shows the lengths, ages, and the year in which the eels joined the population. It is encouraging that the mean back calculated lengths for any particular age class are similar. This result suggests that the back calculation technique is sound. Table 28 shows the mean growth

Table 28. Year, number of eels, mean growth, expected growth from back calculated samples and mean age of each year class.

| Year | No. of cases | Mean growth (cm) | Expected growth (cm) | Mean age (years) |
|---|---|---|---|---|
| 1939 | 1 | 8.82 | 8.82 | 1 |
| 1940 | 1 | 7.21 | 8.79 | 2 |
| 1941 | 1 | 1.58 | 2.43 | 3 |
| 1942 | 2 | 5.20 | 5.55 | 3 |
| 1943 | 2 | 5.55 | 5.50 | 4 |
| 1944 | 2 | 1.87 | 2.25 | 5 |
| 1945 | 4 | 5.55 | 5.48 | 3 |
| 1946 | 5 | 5.11 | 6.11 | 4 |
| 1947 | 5 | 3.09 | 3.53 | 5 |
| 1948 | 9 | 4.84 | 5.12 | 4 |
| 1949 | 10 | 5.27 | 5.43 | 4 |
| 1950 | 13 | 3.96 | 4.23 | 4 |
| 1951 | 13 | 3.36 | 3.66 | 5 |
| 1952 | 15 | 2.53 | 3.01 | 6 |
| 1953 | 20 | 4.35 | 4.41 | 5 |
| 1954 | 24 | 4.79 | 4.56 | 5 |
| 1955 | 24 | 2.85 | 3.18 | 6 |
| 1956 | 26 | 2.40 | 2.58 | 7 |
| 1957 | 29 | 3.15 | 3.15 | 7 |
| 1958 | 33 | 3.49 | 3.39 | 7 |
| 1959 | 38 | 3.39 | 3.55 | 7 |
| 1960 | 56 | 4.67 | 4.75 | 6 |
| 1961 | 67 | 4.99 | 4.91 | 6 |
| 1962 | 86 | 4.30 | 4.41 | 6 |
| 1963 | 96 | 4.07 | 4.06 | 6 |
| 1964 | 104 | 3.20 | 3.23 | 7 |
| 1965 | 109 | 2.86 | 2.82 | 7 |
| 1966 | 116 | 2.79 | 2.67 | 8 |
| 1967 | 120 | 2.46 | 2.54 | 9 |
| 1968 | 123 | 2.14 | 2.28 | 9 |
| 1969 | 124 | 1.99 | 2.06 | 10 |
| 1970 | 124 | 1.98 | 1.86 | 11 |

Table 28. continued

Table 28. continued

| | | | | |
|---|---|---|---|---|
| 1971 | 127 | 1.92 | 1.91 | 12 |
| 1972 | 130 | 2.01 | 2.02 | 13 |
| 1973 | 130 | 1.83 | 1.81 | 14 |
| 1974 | 130 | 1.77 | 1.61 | 15 |
| 1975 | 116 | 1.71 | 1.55 | 16 |
| 1976 | 29 | 1.94 | 1.63 | 14 |

and expected growth for all years covered by the back calculated lengths. The mean age for each year class is also given.

Lake Ellesmere has been exploited by eel fishermen for many years but only recently have catch rates climbed to high levels (Table 29). Heavy exploitation has taken place only since 1968

Table 29. Catch in tonnes of Lake Ellesmere eels.

| Year | Fishing return (inaccurate) | Processers export figures |
|---|---|---|
| 1966 | | |
| 1967 | 5 | - |
| 1968 | 55 | - |
| 1969 | 53 | - |
| 1970 | 35 | - |
| 1971 | 101 | - |
| 1972 | 274 | - |
| 1973 | 283 | - |
| 1974 | 222 | 350 |
| 1975 | 376 | 526 |
| 1976 | 920 | 647 |
| 1977 | 610 | 560 |

and it may be significant that since that date all the years (with the exception of 1969 and 1972) have an actual growth rate that is greater than the expected. Prior to 1968 actual and expected growth fluctuated with no clear pattern. It is reasonable to suggest that the post-1968 pattern is not an artefact but is a direct result of heavy eel cropping.

Removing fish of marketable size will reduce intraspecific competition and increase growth rates. Whether total productivity is greater now than before heavy cropping started is unknown, it seems likely that net production from fewer faster growing fish will be similar to that from a larger slower growing population. No information on eel density before and after intensive fishing is available and, therefore, actual production cannot be computed. If fishing reduces competition to the point where all fish are growing at their maximum rate, any increase in fishing intensity must inevitably lead to a decrease in productivity. Baseline information on eel density must be obtained before a rational

fishing programme can be determined. The method used in this study could be profitably used in most fish population studies.

The growth rates for Lake Ellesmere eels are similar to those found in other studies up until age class 3 or 4, but fall rapidly thereafter (Fig. 12). It seems that young elvers are able to find an adequate food supply but, as soon as they reach more than 20 cm, the supply becomes inadequate to sustain fast growth. Growth rates appear to be improving as the stocks are reduced by fishing. Pantulu and Singh (*loc. cit.*) compare the growth of *A. nebulosa* with results from other eel species given by various authors but it appears that they slightly misinterpreted the information they present. For example, the growth rate presented for *A. a. schmidtii* is based on the work of Cairns (1942). Cairns stated that the first two years of eel life were spent at sea, and he, therefore, started the age/length curve at age three. Pantulu and Singh (*loc. cit.*), as is now customary, did not include seawater life on the axes of their graph and plotted the results of their own study from age 1 (age class 0). The data presented for all the other eel species should, therefore, be displaced two years to the left. When this is done, the growth rate of *A. nebulosa* is not appreciably faster than that of the other species. Burnet (1969b) drew growth curves based on otolith and tag returns for eels from lowland streams. His data, plotted in Fig. 12, shows that stream fish grow at a faster rate than Lake Ellesmere fish. The Lake Ellesmere eel population appears to grow at an extremely slow rate in comparison with other populations of the same species from different habitats and with other species (Ehrenbaum and Marukawa, 1914, Tesch, 1928, Cairns, 1942, Frost, 1945, Sinha and Jones, 1967a, Burnet, 1969 and Rasmussen, 1977). Presumably, this slow growth rate is due to intraspecific competition, but, if this were the case, eels would be expected to migrate out of the population to reduce the pressure if suitable alternatives were available. One of two situations could arise.

i) Eels within the catchment and lake live under conditions of high density and experience intraspecific competition.

ii) Lake Ellesmere has basically a closed population with minimal movement in or out.

If proposition i) is correct, samples of eels taken from the catchment should show similar growth rates to lake fish. If

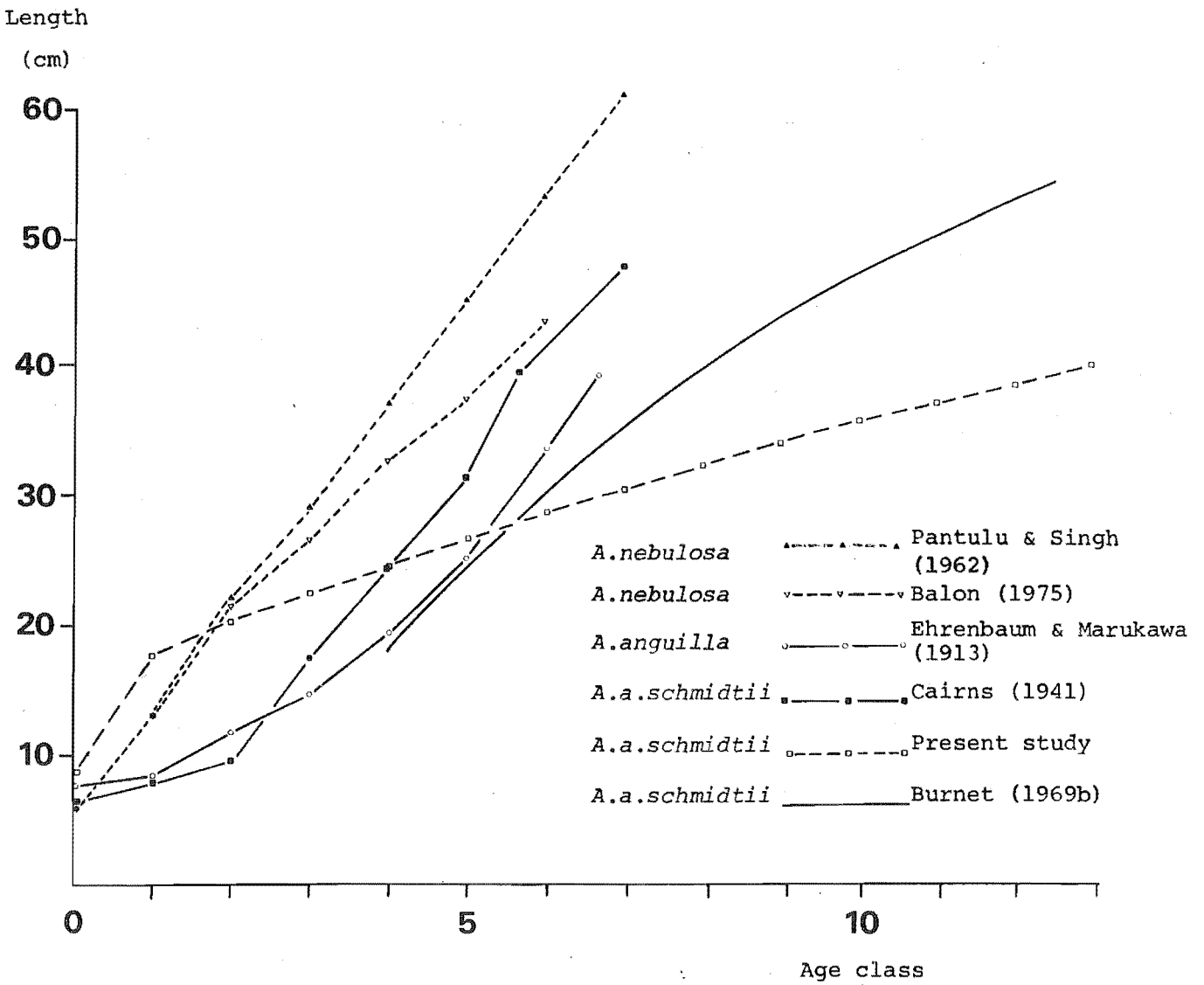


Fig. 12. Growth rates of *Anguilla* sp. compared with those obtained in the present study for *A. a. schmidtii*.

proposition ii) is correct, eels from the catchment area should show appreciably different growth rates from lake fish. These hypotheses make the assumption that the eels from the Taumutu area of the lake are characteristic of the population as a whole.

To test these hypotheses 13 eels were removed from one of the catchment inflows, the Selwyn River, and a back calculated growth curve was fitted from otolith measurements (Fig. 13). These fish were all female, so can be compared with the growth curve for Lake Ellesmere female fish. Eel growth in the Selwyn River from age class 0 to age class 5 was slower than the Lake Ellesmere fish but from age class 5 onwards the Selwyn fish grow faster, which suggests that proposition ii) is correct and migration in and out of the lake is minimal. Tesch (1967, 1973), Vladykov (1971) and Hurley and Donal (1972) have shown that non-migrant eels possess a strong homing instinct. Tesch (1973) found that a 70 km seaward transplantation of eels from a dike in the Ijsselmeer was followed by a 100% return to their home water. Gunning and Shoop (1962) demonstrated a home range of 60-140 m in small streams. In view of the results in the literature and the difference in growth rate between Lake Ellesmere and Selwyn River eels, it seems likely that interchange between the populations is small.

Sex determination in the eel is still not properly understood but coastal regions are correlated with a high proportion of male eels. Tesch (1973) believes that overcrowding in coastal regions produced intraspecific competition and thus low growth rates. Parsons *et al.* (1977) added support to this view after examining the sex ratios of migrant eels from Lough Neagh at different intervals, after the lake was stocked with large numbers of elvers. In the present study, those eels from Lake Ellesmere positively identified as female had a faster growth rate at all stages than those in which the sex could not be determined (undifferentiated). The small sample of eels from the Selwyn River, all female, showed slow growth rate as young fish. Sex in this instance would appear not to be environmentally determined, unless sex is decided as late as age class 4 when rapid growth of these fish commenced.

To enable the growth rate of eels to be expressed in calorific terms, it was necessary to determine length/calorific values for *A. a. schmidtii* (Table 30). These results compare

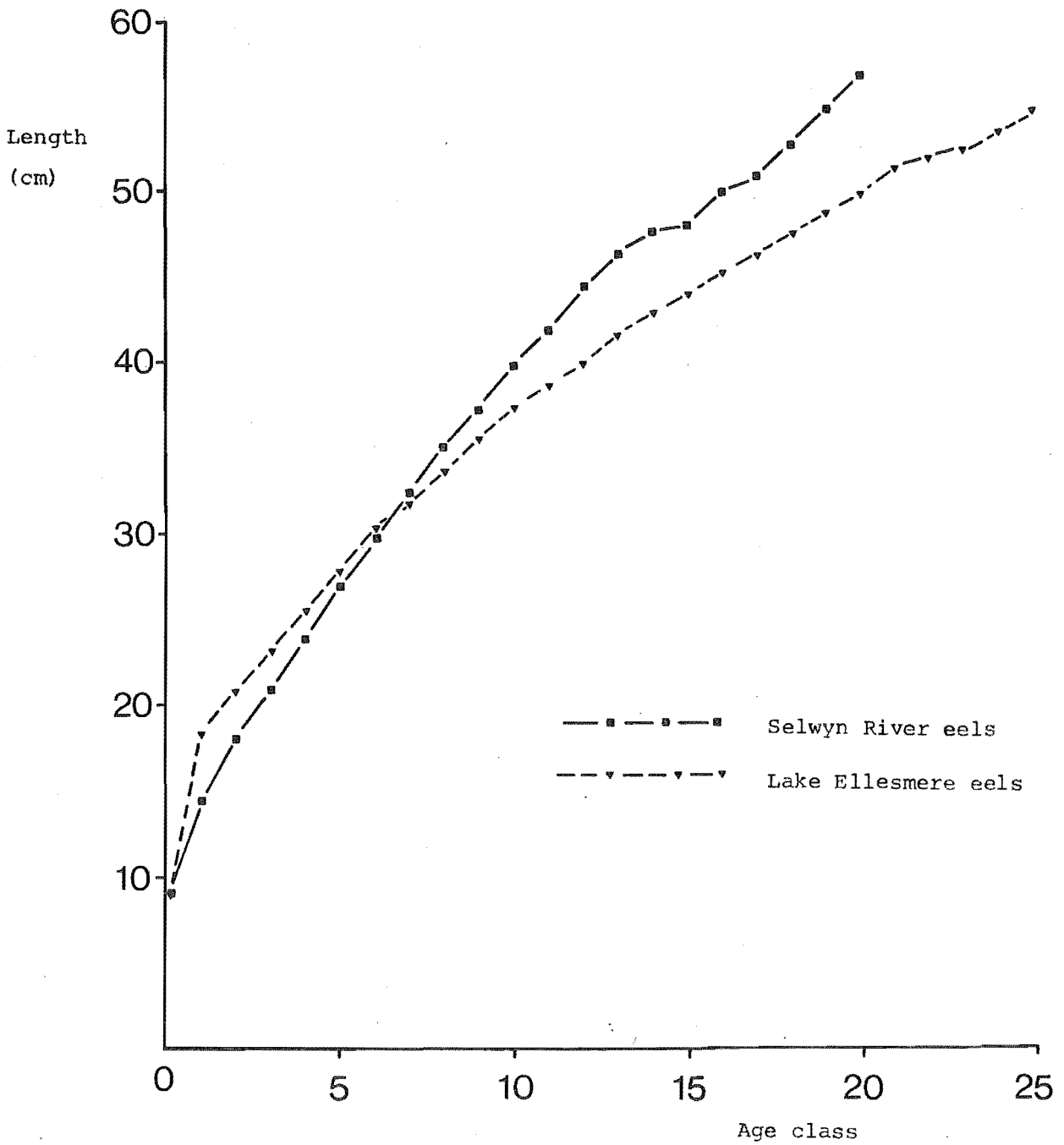


Fig. 13. Back calculated growth rates for Selwyn River, and Lake Ellesmere, female eels.

Table 30. Eel length, wet weight, dry weight, dry weight as a percentage of wet weight, and calorific value ± standard deviation for 11 eels caught in autumn.

| Eel length (cm) | Wet weight (g) | Dry weight (g) | Dry weight as percentage of wet weight | Calorific value (j/g dry weight) ± S.E. |
|---|---|---|---|---|
| 45.0 | 170 | 49.2 | 28.9 | 22 907 ± 101.3 |
| 43.5 | 144 | 38.5 | 26.7 | 21 977 ± 1507 |
| 44.0 | 180 | 44.6 | 24.7 | 21 123 ± 728.5 |
| 41.3 | 134 | 31.1 | 23.2 | 19 938 ± 824.8 |
| 41.0 | 151 | 52.1 | 34.5 | 26 265 ± 352.5 |
| 49.2 | 234 | 62.0 | 26.4 | 24 598 ± 782.9 |
| 43.4 | 178 | 57.5 | 32.3 | 25 265 ± 1178.2 |
| 47.3 | 210 | 58.8 | 28.0 | 21 793 ± 510.8 |
| 56.0 | 354 | 109.7 | 30.9 | 28 283 ± 295.6 |
| 58.0 | 440 | 148.4 | 33.7 | 29 116 ± 728.5 |
| 64.7 | 558 | 169.6 | 30.3 | 27 994 ± 715.9 |

favourably with the 25,122 j given by Crossland (1972) in his study on the energy budget of *A. a. schmidtii*. As the eels used in the determinations were all caught in autumn and as their condition factor is highest in autumn (see Chapter 1), these results should represent maximum values.

SUMMARY

As back calculated lengths compare favourably with lengths of fish of known age at time of capture, back calculation can be used to describe the growth of Lake Ellesmere eels. Growth curves fitted to back calculation data show that female fish grow faster than undifferentiated fish and both show much lower growth rates than those found in other reported studies. The von Bertalanffy growth equation described the growth rates of Lake Ellesmere fish very well. Since the onset of heavy fishing pressure on the eel population, growth rates appear to have improved, due probably to reduced intraspecific competition. Selwyn River female fish grew faster than Ellesmere female fish from age class 4 onwards, which suggests that interchange between the two populations is small. Although otoliths were assigned different readability indices, no differences in growth rates between the readability groups were found. It appears that the different readability indices are determined by the preparation of the otolith rather than an intrinsic feature of the otolith. Calorific values were determined for 11 eels caught in autumn.

# CHAPTER THREE. GASTRIC EVACUATION, DAILY RATION AND ENERGY BUDGET

## INTRODUCTION

Experiments were conducted to determine the gastric evacuation rate of *A. australis schmidtii* when fed the prey organisms that occurred most frequently in stomach analyses. Different temperatures and ration sizes were used to determine the effects of variations in these factors on gastric evacuation. Gross assimilation efficiencies were also calculated by collecting faeces and comparing the calorific values of the faeces with the calorific value of food given to the eel.

Gastric evacuation rates are required before daily ration can be calculated. Many different approaches have been utilised for fish. Gastric evacuation figures for fish in their natural environment are probably the most useful but are also the hardest to obtain. Bajkov (1935), Darnell and Meierotto (1962), Seaburg and Moyle (1964), Wissing (1974), Staples (1975) and others have used variations of the same method to arrive at figures for intensity of food consumption, daily ration or evacuation rates. A large number of fish are captured and returned to the water in food-free containers. A first group is killed and preserved immediately for later analysis of degree of stomach fullness. Similar sized groups are killed after they have been held in food-free confinement for known periods of time. The successive measurements indicate the average number of hours required for percentage reduction of stomach contents from time zero through until 100% evacuation. Major shortcomings of this method are the degree of effort required to catch a large number of fish and the lack of control over variables such as temperature.

Laboratory digestion experiments are more easily controlled but results cannot necessarily be extrapolated to field conditions. Several different laboratory approaches have been used. Hunt (1960), Windell (1966, 1967, 1971), Windell and Norris (1969), Windell *et al.* (1969), Brett and Higgs (1970), Elliott (1972), Swenson and Smith (1973), Griffiths (1976) and others killed fish,which had voluntarily fed on known amounts of food, at successive time intervals and measured depletion of stomach contents. Hunt also force-fed fish and, although he stated that

no differences were observed between force-fed and voluntarily-fed fish, he based this statement on only 13 voluntarily-fed fish and on only one of the two species studied. Molnar and Tolg (1962) force-fed fish and followed digestion by X-raying the experimental fish at intervals and monitoring the disappearance of bony parts from the stomach. Although natural prey species were used for the force-feeding, no attempt was made to determine what effect force-feeding had on evacuation rates. Seaburg and Moyle (1974) force-fed pike (*Esox lucius*) with perch but encountered problems with regurgitation. They removed perch from pike stomachs using a small water operated pump. The effect of this rather rough treatment was not studied. Windell (1966), in his study on the bluegill sunfish *Lepomis macrochirus*, force-fed fish with meal worms and compared the gastric evacuation with a voluntarily-fed control group. He showed that decreased digestion took place in force-fed fish, and the coefficient of variation was much higher. Griffiths (1976) also force-fed perch, *Perca fluviatilis* but anaesthetised them first using benzocaine. This procedure presumably reduces stress as no significant differences were obtained between voluntarily-fed and force-fed fish.

In the present study, eels were trained to voluntarily feed on the bully, *Gobiomorphus cotidianus*. As this took nearly a year, it became evident that force-feeding must be used in subsequent experiments. To quantify the effect of force-feeding, bullies were force-fed to the experimental eels. Subsequent experiments to find the effect of ration size on evacuation rates utilised the isopod, *Austridotea annectens* in force-feeding experiments. The mollusc, *Potamopyrgus antipodarum* was also used to force-feed eels to determine any differences in evacuation rate from *A. annectens*.

METHODS

It was not possible to obtain large numbers of eels for use in stomach evacuation experiments in the field. It was decided, therefore, to conduct digestion experiments in the laboratory. To ensure results were as realistic as possible, only natural prey organisms were used.

Temperature is one of the most important factors determining gastric evacuation in fish (Elliott, 1972), so a constant temperature room was used for all experiments. Preliminary experiments were conducted at 20°C ± 1°C, which is the highest temperature normally reached in Lake Ellesmere (Fig. 2).

Ten round blue plastic tanks, with a capacity of approximately 40 l, were made by cutting the bottoms off 40-gallon plastic drums. These containers previously contained a tanning compound used in the leather industry and, therefore, required careful cleaning. Each tank was tested by keeping a small goldfish, *Carassius auratus*, in it for five weeks, during which time no deaths occurred. As goldfish are more sensitive to water conditions than eels, it was assumed that the tanks were clean. The tanks were each filled with 10 l of tap water (artesian) and placed in two rows of three at ground level and two rows of two immediately above in a robust "angle iron" support structure. A single 120 cm fluorescent 60 watt dayglo tube was suspended above each bank of tanks. A summertime lighting regime of 16 hours light, 8 hours dark was controlled by a time switch. Each tank was provided with an airstone to keep the water well saturated with oxygen. Lengths of black alkathene piping 25 cm long and 5 cm in diameter, weighted with strips of lead heat-sealed into thin plastic tubes, gave the eels shelter.

Eels were obtained from the Selwyn River (which drains into Lake Ellesmere) using fyke nets or, when catch rates were poor, from commercial eel fishermen at Taumutu. All fish were treated for disease by dosing them with furanace* at a concentration of 1 part per million.

* Abbott Laboratories (N.Z.) Ltd, Lower Hutt, New Zealand.

Stomach analyses (see chapter 1) indicated that *Gobiomorphus cotidianus* and other fish, *Austridotea annectens*, *Tenagomysis chiltoni*, *Potamopyrgus antipodarum* and *Chironomus zealandicus* larvae were the most important food organisms. Experiments were carried out using some of these species to determine the length of time required for ingested prey organisms to reach the different degrees of digestion found in stomach samples. Evacuation rates were not determined for *T. chiltoni* and *C. zealandicus* as it was considered that *A. annectens* could provide an estimate for other species of small size.

Voluntarily-fed eels were used in the first experiment. Initially, eels were weighed and acclimatised to the experimental tanks for several days. They were tempted into feeding by offering live bullies (*G. cotidianus*); bullies were prevented from escaping by holding their caudal fin with a pair of forceps. Eels were extremely shy, probably partly due to periodic vibrations caused by the closing of heavy doors of adjacent constant temperature rooms. Up to six weeks was required before most eels would feed voluntarily. When voluntary feeding occurred, eels were fed and then starved for 48 hours to clear the stomach.

To standardise meal size, bullies were selected to give a ration size of 1 mg dry weight of bully per g wet weight of eel. Each bully was offered to experimental eels and the time of ingestion recorded. Eels were sacrificed after a known time interval and the stomach contents removed, placed in containers of known weight, and dried to constant weight at 70°C. The dried weight of each bully was compared with its pre-ingested dry weight (determined from wet weight/dry weight measurements) to give percentage evacuation. Experiments were run for 1 1/2, 3, 5, 8, 10, 12 and 15 hours and a regression line fitted to percentage evacuation/time data.

Because these voluntarily-fed experiments with bullies at 20°C took nearly a year to complete, it became evident that to improve the speed with which experiments were completed, force-feeding must be adopted. Eels were anaesthetised using benzocaine, and force-fed by pushing the bullies down the oesophagus with a long pair of forceps. The progress of the bully through the oesophagus could be seen by the movement of the bulge down the eel. This method of feeding ensured that the food was not forced too far into the eel stomach. Occasionally regurgitation

occurred. Experimental runs for 7, 9, 11, 15 and 18 hours were carried out at a ration level of 1 mg dry weight of bully per g wet weight of eel. The fitted regression line was parallel to the voluntarily-fed regression line, indicating that the evacuation rate was identical. There was, however, a marked time lag of 5.1 hours, presumably due to the effect of force-feeding. Observation of anaesthetised eels showed that normal orientation behaviour was achieved only after one to two hours. Before this time most eels lay belly up without moving on the bottom of the tanks. The time lag of 5.1 hours was used as a correction factor for subsequent force-feeding experiments.

*A. annectens* and *P. antipodarum* were force-fed to eels by placing the food animals inside a fired glass tube of 7.6 mm internal diameter, except that for eels with a particularly narrow oesophagus a tube of 5 mm internal diameter was used instead. Anaesthetised eels were held by the lower jaw with forceps and the tube inserted down the oesophagus. When the bulge indicating the end of the tube had reached the position of the stomach, a tightly fitting glass rod was placed inside the tube and used as a plunger to force food into the stomach.

Eels were fed at a ration level of 0.4 mg dry weight of food species per g wet weight of eel, except for *A. annectens* which was fed at ration levels of 0.2, 0.4 and 0.8 mg per g wet weight of eels. Experimental runs were done for 6, 7.3, 8, 10 and 12 hours for *A. annectens* and for 6, 8 and 10 hours for *P. antipodarum*.

To determine assimilation efficiency special force-fed runs for each food species were carried out at 20°C and the fish observed until defaecation took place. Faeces were collected with a bulb pipette, dried to a constant weight at 70°C, and bomb calorimeter pellets made. Calorific determinations were made and total calorific values of faeces calculated. Gross assimilation efficiency was determined by comparing the calorific value of the force-fed prey species with the total calorific value of the solid waste products. No attempts were made to measure soluble waste products. This general procedure was similar to that of Kelso (1972), Solomon and Brafield (1972) and Wissing (1974).

## RESULTS AND DISCUSSION

### Feeding experiments

Because eels were often difficult to obtain, there was occasionally a substantial range in the wet weights of experimental fish. For the eels that fed voluntarily on bullies (*G. cotidianus*) the range was 187-391 g. Smaller eels would not voluntarily feed and, therefore, could not be used. In later experiments using invertebrates, the range was 143-562 g. There are conflicting reports in the literature about the effect of fish size on evacuation rate. Seaburg and Moyle (1964) contend that small fish digest food more rapidly than large fish and Steigenberger and Larkin (1974) found no consistent differences in rate of digestion by different sizes of squawfish. Jobling *et al.* (1977) have shown that evacuation rate of food, expressed as percent of body weight, is slower in large fish than in small fish. The results presented by these authors are at variance with the rest of the literature but it is possible that their results are species specific. Windell (1966) found no difference in evacuation time between large and small fish when fed a standard meal based on a proportion of the body weight, which implies that large fish must evacuate food at a higher rate. Tyler (1970) found that small cod evacuated food at a slower rate than large cod. Elliott (1972) has shown that gastric evacuation in brown trout did not vary in the size range 20-30 cm. Swenson and Smith (1973) found increased evacuation rate with increased fish size in walleye. There is no published information available on eel evacuation rates as far as is known, so there is nothing upon which to base any of the experiments in this chapter. The majority of the literature suggests that evacuation times for meal sizes that are proportional to fish size should be directly comparable. Rates in terms of mg/depletion per hour may well be different for different sized fish but percentage weight reduction of the amount initially fed/hour should be similar for fish of different size ranges. Therefore, the basic assumption underlying all evacuation and assimilation work in this study is that evacuation and assimilation rates of meals, expressed as percentage of eel body weight, are directly comparable. Results for voluntarily-fed fish, showing percentage retention of food

given for different time intervals after feeding are given in Table 31. A least squares regression was computer fitted to the means using a semi-logarithmic transformation. Windell *et al.* (1976) found that this method consistently gave the best results when applied to the gastric evacuation rate of rainbow trout. The equation was;

$$\log_e(\text{percent retention}) = -0.00318\ (\text{time in mins}) + 5.07695 \qquad 1.$$

The correlation coefficient was 0.9630.
One hundred percent retention derived from the regression occurs at 2 hours 28 minutes. In other words, evacuation does not start until after that time interval. A time lag is also found in other studies (Hunt, 1960, Windell and Norris, 1969, and Steigenburger and Larkin, 1974).

The results from force-feeding experiments using *G. cotidianus* are given in Table 32. A least squares regression, computer fitted to the means, gave the following equation with a correlation coefficient of 0.9145.

$$\log_e(\text{percent retention}) = -0.00300\ (\text{time in mins}) + 5.9692 \qquad 2.$$

The slope, -0.00300, is almost identical to the -0.00318 for the voluntarily-fed fish, so it is reasonable to assume that the voluntarily-fed fish and the force-fed fish have the same gastric evacuation rates.

The onset of evacuation, determined by equating -0.00300 (time) + 5.9692 to $\log_e(100)$ took place 7 hours and 34 minutes after force-feeding. As voluntarily-fed fish took only 2 hours and 28 minutes before the onset of evacuation, this delay is presumably due to the effects of force-feeding and anaesthetising. The difference between the two lag times of 306 minutes was used to correct for force-feeding in all subsequent experiments. Soivio *et al.* (1977) discuss the physiological effects of anaethetising rainbow trout with benzocaine, but what effect the anaesthetic has on evacuation rate was not studied. Other studies show that force-feeding slows evacuation rate (Windell, 1966, Griffiths, 1976).

Table 31. Percentage retention of voluntarily fed meals of *G. cotidianus* for different time intervals after feeding. Meal sizes and size of eel are also given as is the mean ($\overline{Y}$) ± the standard error of the mean ($S\overline{Y}$).

| Time interval (hours) | Retention (%) | Eel size (g wet weight) | Meal size (mg/g wet weight of eel) |
|---|---|---|---|
| 1.5 | 94.9 | 334 | 1.58 |
| | 95.1 | 343 | 1.17 |
| | 94.8 | 309 | 1.27 |
| | 86.7 | 312 | 1.26 |
| | $\overline{Y}$ = 92.8 ± 23.2 | | |
| 3 | 83.5 | 280 | 0.94 |
| | 79.5 | 248 | 1.06 |
| | 83.3 | 276 | 1.13 |
| | 70.6 | 187 | 1.30 |
| | $\overline{Y}$ = 79.2 ± 19.8 | | |
| 5 | 63.7 | 360 | 1.4 |
| | 64.8 | 357 | 1.4 |
| | 75.7 | 304 | 1.2 |
| | 61.8 | 279 | 1.3 |
| | 71.6 | 277 | 1.1 |
| | 52.7 | 247 | 1.2 |
| | 49.4 | 259 | 1.1 |
| | $\overline{Y}$ = 62.8 ± 8.9 | | |
| 8 | 53.1 | 391 | 1.2 |
| | 40.5 | 265 | 1.5 |
| | 47.3 | 338 | 1.3 |
| | 59.4 | 340 | 1.2 |
| | 57.5 | 268 | 1.2 |
| | 51.8 | 240 | 1.3 |
| | $\overline{Y}$ = 51.6 ± 8.6 | | |
| 10 | 32.6 | 370 | 1.2 |
| | 49.3 | 356 | 1.1 |
| | 16.7 | 349 | 0.9 |
| | 24.2 | 318 | 1.0 |

Table 31 continued

Table 31 continued

| | | | |
|---|---|---|---|
| | 30.4 | 299 | 1.0 |
| | 31.6 | 267 | 1.2 |
| | 22.7 | 279 | 0.9 |
| | $\bar{Y}$ = 29.6 ± 4.2 | | |
| 12 | 4.0 | 242 | 1.2 |
| | 2.5 | 262 | 1.3 |
| | 17.6 | 218 | 1.5 |
| | 14.5 | 248 | 1.4 |
| | $\bar{Y}$ = 9.6 ± 2.4 | | |
| 15 | 11.8 | 389 | 1.0 |
| | 6.0 | 372 | 1.1 |
| | 4.3 | 390 | 0.9 |
| | $\bar{Y}$ = 7.3 ± 2.4 | | |

Table 32. Percentage retention of force-fed meals of *G. cotidianus* for different time intervals after feeding. Meal sizes and size of eel are also given as is the mean ($\bar{Y}$) ± the standard error of the mean ($S\bar{Y}$).

| Time interval (hours) | Retention (%) | Eel size (g wet weight) | Meal size (mg/g wet weight of eel) |
|---|---|---|---|
| 7 | 81.5 | 413 | 1.3 |
| | 89.7 | 412 | 1.5 |
| | 72.3 | 313 | 0.9 |
| | 96.7 | 529 | 1.2 |
| | $\bar{Y}$ = 85 ± 21.2 | | |
| 9 | 81.8 | 493 | 1.2 |
| | 72.7 | 317 | 1.1 |
| | 91.8 | 268 | 1.2 |
| | 54.7 | 238 | 0.9 |
| | $\bar{Y}$ = 75.2 ± 18.8 | | |
| 12 | 65.2 | 539 | 0.9 |
| | 67.3 | 551 | 0.9 |
| | 66.8 | 357 | 1.1 |
| | 67.4 | 311 | 1.1 |
| | 37.8 | 548 | 1.1 |
| | 60.9 | 295 | 1.0 |
| | 58.8 | 243 | 1.3 |
| | 58.9 | 360 | 1.6 |
| | 65.3 | 398 | 1.5 |
| | $\bar{Y}$ = 60.9 ± 6.7 | | |
| 15 | 13.4 | 298 | 1.2 |
| | 16.5 | 226 | 1.2 |
| | 27.8 | 322 | 1.3 |
| | 43.8 | 317 | 1.5 |
| | 60.2 | 282 | 1.4 |
| | 53.0 | 394 | 1.4 |
| | 65.5 | 447 | 1.4 |
| | $\bar{Y}$ = 40 ± 5.7 | | |

Table 32 continued

Table 32 continued

| | | | |
|---|---|---|---|
| 18 | 33.9 | 498 | 1.0 |
| | 0.0 | 340 | 0.9 |
| | 10.9 | 385 | 1.0 |
| | 0.0 | 540 | 1.1 |
| | 15.2 | 440 | 1.0 |
| | $\bar{Y} = 12 \pm 2.4$ | | |

It was originally planned to force-feed eels with bullies in gastric evacuation experiments at other temperatures. When this experiment was attempted, it rapidly became evident that eel recovery rate, from the effects of benzocaine, was also temperature-dependent. This effect negated the use of the 5.1 hour correction factor. Attempts to use time taken for restoration of eel equilibrium after anaesthesia at different temperatures as a correction factor to the time lag were not successful. There is, therefore, no linear relationship between restoration of eel equilibrium and recovery of digestive faculties. It was reluctantly decided, therefore, to try to use voluntarily-fed eels at the different temperatures. No eels would feed at 10°C or 25°C and after three months of experimentation with 16 eels, only one had fed at 15°C. The effect temperature has on gastric evacuation rate must be known before evacuation rates of eels, in the wild, can be determined. However, Elliott (1972), Jones (1974) and Windell *et al.* (1976) have all shown that gastric evacuation rates follow the normally accepted $Q_{10}$ law, i.e. chemical reactions double for every 10°C rise in temperature. The failure of this section of experimental work did not, therefore, prevent assumptions being made about the effect of temperature on gastric evacuation.

Fish are likely to be evacuated at different rates from small invertebrates. Ration level is also likely to affect evacuation rate (Seaburg and Moyle, 1964, Windell, 1966, Tyler, 1970, Elliott, 1972, Swenson and Smith, 1973, Steigenberger and Larkin, 1974, and Jobling *et al.*, 1977). Therefore, experiments were carried out using *A. annectens* as the prey organism fed at ration levels of 0.2, 0.4 and 0.8 mg dry weight/g wet weight of eel. As force-feeding was used, the time lag of 5.1 hours was subtracted. Results are presented in Tables 33, 34 and 35.

When least squares regressions were computer fitted to the means, the following equations were obtained.

0.2 mg ration

$$\log_e(\text{percent retention}) = -0.01029\ (\text{time in minutes}) + 4.82271$$

Correlation coefficient was 0.9308.

Table 33. Percentage retention of *A. annectens* fed to eels at a ration level of approximately 0.2 mg/g wet weight of eel. The mean ($\bar{Y}$) ± the standard error of the mean ($S\bar{Y}$) is also given.

| Time interval (hours) | Retention (%) | Eel size (g wet weight) | Ration size (mg/g wet weight of eel) |
|---|---|---|---|
| 0.9 | 67.6 | 420 | 0.2 |
| | 53.1 | 354 | 0.2 |
| | 83.4 | 249 | 0.2 |
| | 64.2 | 240 | 0.2 |
| | 80.3 | 152 | 0.17 |
| | 78.0 | 149 | 0.18 |
| | 37.7 | 169 | 0.17 |
| | $\bar{Y}$ = 66.3 ± 5.7 | | |
| 2.2 | 40.2 | 548 | 0.19 |
| | 0.0 | 442 | 0.19 |
| | 60.3 | 562 | 0.20 |
| | 18.2 | 324 | 0.20 |
| | 10.6 | 345 | 0.19 |
| | 0.0 | 277 | 0.20 |
| | 37.7 | 397 | 0.19 |
| | 36.8 | 322 | 0.20 |
| | $\bar{Y}$ = 25.4 ± 7.1 | | |
| 2.9 | 0.0 | 364 | 0.19 |
| | 0.0 | 320 | 0.20 |
| | 30.5 | 263 | 0.20 |
| | 7.7 | 274 | 0.20 |
| | 13.6 | 285 | 0.20 |
| | 25.5 | 315 | 0.20 |
| | 0.0 | 396 | 0.20 |
| | 45.2 | 310 | 0.20 |
| | 48.2 | 396 | 0.20 |
| | $\bar{Y}$ = 18.9 ± 6.0 | | |
| 4.9 | 45.0 | 244 | 0.16 |
| | 4.5 | 242 | 0.17 |
| | 0.0 | 299 | 0.19 |

Table 33 continued

Table 33 continued

| | | | |
|---|---|---|---|
| | 39.0 | 290 | 0.17 |
| | 29.0 | 290 | 0.17 |
| | 0.0 | 163 | 0.20 |
| | 24.0 | 207 | 0.15 |
| | 6.4 | 261 | 0.18 |
| | 0.0 | 235 | 0.17 |
| | 9.8 | 302 | 0.18 |
| | $\bar{Y}$ = 15.7 ± 5.1 | | |
| 6.9 | 0.0 | 215 | 0.19 |
| | 0.0 | 217 | 0.19 |
| | 0.0 | 310 | 0.19 |
| | 0.0 | 300 | 0.19 |
| | 0.0 | 238 | 0.21 |
| | 5.4 | 265 | 0.19 |
| | 0.0 | 230 | 0.18 |
| | $\bar{Y}$ = 0.77 ± 0.7 | | |

Table 34. Percentage retention of *A. annectens* fed to eels at a ration level of approximately 0.4 mg/g wet weight of eel. The mean ($\bar{Y}$) ± the standard error of the mean ($S\bar{Y}$) is also given.

| Time interval (hours) | Retention (%) | Eel size (g wet weight) | Ration size (mg/g wet weight of eel) |
|---|---|---|---|
| 0.9 | 88.9 | 274 | 0.32 |
| | 61.5 | 308 | 0.40 |
| | 68.1 | 226 | 0.34 |
| | 83.5 | 194 | 0.33 |
| | 73.0 | 251 | 0.45 |
| | 82.0 | 304 | 0.50 |
| | 94.0 | 235 | 0.50 |
| | $\bar{Y}$ = 78.7 ± 4.0 | | |
| 2.2 | 0.0 | 533 | 0.39 |
| | 52.5 | 191 | 0.40 |
| | 48.9 | 337 | 0.38 |
| | 58.5 | 457 | 0.41 |
| | 44.6 | 220 | 0.40 |
| | 41.6 | 290 | 0.42 |
| | $\bar{Y}$ = 41 ± 7.8 | | |
| 2.9 | 51.5 | 513 | 0.39 |
| | 0.0 | 417 | 0.40 |
| | 0.0 | 439 | 0.40 |
| | 0.0 | 422 | 0.39 |
| | 9.3 | 420 | 0.40 |
| | 64.0 | 247 | 0.49 |
| | 62.0 | 325 | 0.50 |
| | 50.5 | 290 | 0.40 |
| | 71.9 | 234 | 0.40 |
| | $\bar{Y}$ = 34.3 ± 9.7 | | |
| 4.9 | 6.6 | 173 | 0.39 |
| | 25.2 | 227 | 0.41 |
| | 0.0 | 251 | 0.40 |
| | 0.0 | 260 | 0.39 |
| | 0.0 | 244 | 0.41 |

Table 34 continued

Table 34 continued

| | | | |
|---|---|---|---|
| | 0.0 | 275 | 0.40 |
| | 0.0 | 312 | 0.40 |
| | 46.9 | 325 | 0.39 |
| | $\bar{Y}$ = 9.8 ± 5.7 | | |
| 6.9 | 0.0 | 228 | 0.39 |
| | 16.8 | 155 | 0.43 |
| | 0.0 | 264 | 0.39 |
| | 0.0 | 220 | 0.40 |
| | 0.0 | 157 | 0.42 |
| | 1.8 | 160 | 0.42 |
| | 0.0 | 230 | 0.39 |
| | $\bar{Y}$ = 2.6 ± 2.1 | | |

Table 35. Percentage retention of *A. annectens* fed to eels at a ration level of approximately 0.8 mg/g wet weight of eel. The mean ($\bar{Y}$) ± the standard error of the mean ($S\bar{Y}$) is also given.

| Time interval (hours) | Retention (%) | Eel size (g wet weight) | Ration size (mg/g wet weight of eel) |
|---|---|---|---|
| 1.4 | 74.2 | 191 | 0.80 |
| | 72.5 | 270 | 0.79 |
| | 49.5 | 191 | 0.80 |
| | 59.2 | 143 | 0.80 |
| | 94.9 | 187 | 0.79 |
| | 53.7 | 233 | 0.80 |
| | 82.3 | 187 | 0.79 |
| | 85.8 | 175 | 0.80 |
| | $\bar{Y}$ = 71.5 ± 5.3 | | |
| 2.9 | 67.1 | 150 | 0.88 |
| | 88.3 | 165 | 0.86 |
| | 87.2 | 354 | 0.87 |
| | 67.0 | 217 | 0.98 |
| | 75.8 | 147 | 0.86 |
| | 67.0 | 224 | 0.88 |
| | 75.8 | 147 | 0.86 |
| | 67.0 | 224 | 0.88 |
| | 65.8 | 158 | 0.87 |
| | 62.2 | 313 | 0.87 |
| | 31.2 | 260 | 0.88 |
| | $\bar{Y}$ = 68.5 ± 4.3 | | |
| 3.9 | 58.5 | 188 | 0.70 |
| | 51.5 | 160 | 0.78 |
| | 40.7 | 188 | 0.70 |
| | 42.0 | 180 | 0.77 |
| | 13.0 | 317 | 0.79 |
| | 0.0 | 235 | 0.80 |
| | 50.6 | 164 | 0.81 |
| | 44.0 | 280 | 0.80 |
| | 66.3 | 234 | 0.80 |
| | Y = 40.7 ± 6.6 | | |

Table 35 continued

Table 35 continued

| | | | |
|---|---|---|---|
| 4.9 | 20.8 | 213 | 0.81 |
| | 0.0 | 200 | 0.81 |
| | 16.4 | 162 | 0.77 |
| | 45.7 | 233 | 0.79 |
| | 18.1 | 177 | 0.81 |
| | 0.0 | 203 | 0.79 |
| | 8.6 | 200 | 0.81 |
| | 32.5 | 166 | 0.79 |
| | 12.0 | 187 | 0.80 |

$\overline{Y} = 17.1 \pm 4.6$

0.4 mg ration

$$\log_e(\text{percent retention}) = -0.00982\ (\text{time in minutes}) + 5.03945$$

Correlation coefficient was 0.9936.

0.8 mg ration

$$\log_e(\text{percent retention}) = -0.00694\ (\text{time in minutes}) + 5.13387$$

Correlation coefficient was 0.9168.

There were no obvious signs of gastric digestion *per se* in the stomachs examined. The isopods seemed to remain almost intact and pass through the pyloric sphincter complete. It seems that the stomach is more of a storage organ than a digestive organ with small items. This observation has also been made by Crossland (1972). The actual gastric evacuation time, from time of feeding to total evacuation of the gut, was almost identical for all ration levels. There was, however, a varying lag time before the onset of evacuation (Table 36). It is

Table 36. Lag time before the onset of evacuation.

| | Ration size (mg/g wet weight of eel) | | |
|---|---|---|---|
| | 0.2 | 0.4 | 0.8 |
| lag time (mins) | 21 | 44.2 | 76.8 |

conceivable that the delay in onset of evacuation is due to the effects of force-feeding. As a ration level of 0.2 mg was the biggest load the fired glass tube could administer without crushing the contents, ration levels of 0.4 and 0.8 mg required twice and four times as much handling of the eels. Elapsed times from the onset of evacuation to complete emptying were regressed against ration level, using a Bartletts 3 group regression fitted by computer, to describe the effect of ration size on evacuation rate. This gave the equation;

$$\log(\text{time}) = 13.3512(\text{ration size}) - 3.4732$$

An experiment was also carried out using *P. antipodarum* as the

prey organism to see whether different invertebrate species were evacuated at different rates (Table 37).

When a least squares regression was fitted by computer to the means, the following equation was calculated.

$$\log_e(\text{percent retention}) = -0.00587\ (\text{time in minutes}) + 4.5855$$

The correlation coefficient was 0.997.
The total evacuation time was similar in slope to the 0.8 mg isopod result but the rate is lower than the 0.8 mg isopod evacuation rate. The reason for this is not known. It is possible that the eel stomach can only eject one piece of matter per contraction, regardless of the size of the particle. If this were so it would in part explain the much longer time required for total gastric evacuation of *P. antipodarum*, as there are many more *P. antipodarum* in a given standard meal than there are *A. annectens*. The different result for evacuation of *P. antipodarum* suggests that evacuation rates may be food species specific. If this is the case, models of gastric evacuation must be developed for the different prey species in the diet of any fish. Kitchell and Windell (1968) found differences in evacuation rate for dragonfly larvae and meal worms when they were fed to pumpkinseed sunfish. Windell and Norris (1969) found differences in gastric evacuation rate between oligochaetes and commercial trout pellets fed to rainbow trout. Elliott (1972) also found differences in evacuation rate for various groups of organisms fed to brown trout. Within each group the prey species exhibited a similar rate of gastric evacuation but between groups comparisons showed differences.

If the results obtained for evacuation rate with respect to temperature when bullies were used as prey organisms are applicable to invertebrates as well, a model might be evolved that would determine ingestion times of all prey organisms at different ration sizes. But because bullies are large organisms that must be mechanically broken down before they will pass through the pyloric sphincter, comparisons with the small easily evacuated invertebrates would not be valid. It was, therefore, not possible to produce a model describing eel evacuation of different ration levels of prey species at different temperatures.

Table 37. Percentage retention of *P. antipodarum* at a ration level of approximately 0.8 mg/g wet weight of eel. The mean ($\bar{Y}$) ± the standard error of the mean ($S\bar{Y}$) is also given.

| Time interval (hours) | Retention (%) | Eel size (g wet weight) | Ration size (mg/g wet weight of eel) |
|---|---|---|---|
| 0.9 | 90.2 | 225 | 0.80 |
| | 43.7 | 160 | 0.80 |
| | 83.0 | 326 | 0.81 |
| | 92.0 | 290 | 0.80 |
| | 90.4 | 335 | 0.80 |
| | 75.9 | 377 | 0.80 |
| | 59.9 | 251 | 0.80 |
| | 20.5 | 300 | 0.80 |
| | 85.4 | 245 | 0.80 |
| | 92.4 | 137 | 0.80 |
| | 30.5 | 388 | 0.80 |
| | 90.1 | 368 | 0.80 |
| | 51.9 | 335 | 0.80 |
| | $\bar{Y}$ = 69.6 ± 6.7 | | |
| 2.9 | 42.0 | 147 | 0.80 |
| | 34.0 | 297 | 0.80 |
| | 50.1 | 167 | 0.80 |
| | 9.9 | 320 | 0.80 |
| | 35.0 | 134 | 0.80 |
| | 24.0 | 184 | 0.80 |
| | 35.4 | 300 | 0.80 |
| | 68.0 | 126 | 0.80 |
| | $\bar{Y}$ = 37.3 ± 5.6 | | |
| 4.9 | 0.0 | 161 | 0.80 |
| | 3.0 | 143 | 0.80 |
| | 58.4 | 225 | 0.80 |
| | 27.6 | 327 | 0.80 |
| | 0.0 | 339 | 0.80 |
| | 0.0 | 142 | 0.80 |
| | 19.3 | 179 | 0.80 |
| | 0.0 | 355 | 0.80 |
| | 56.8 | 224 | 0.80 |
| | 5.7 | 405 | 0.80 |
| | $\bar{Y}$ = 17.0 ± 6.9 | | |

Because the calculated pre-ingested weight of many invertebrates was less than the actual weight removed from eel stomachs (see page 45, chapter 1), percentage digestion for invertebrates could not be determined. Furthermore, visual examination, after several hours in the stomach, of the two species of invertebrate used in feeding experiments showed that little, if any, digestion had taken place. The concept of percentage digestion is thus meaningless for small invertebrates. The results presented here indicate, therefore, that more experiments involving different ration sizes and temperatures are unlikely to produce a comprehensive model of eel evacuation.

Daily ration

Daily ration can be calculated using the formula developed by Fortunatova (1950). This formula assumes the following conditions:

1. The fish typically ingest a large quantity of food at a time, but not more often than once a day and frequently less often.
2. No fish feeds again until its previous meal has passed out of its stomach.
3. The length of time required for complete gastric digestion is known.

Condition 1. is met with as far as >50.1 cm eels are concerned. Over 90% of their diet is in the form of fish. For the 40.1-50 cm size class eels over 60% of the diet is in the form of fish, so the condition is met with for most of this size class also. The ⩽40 cm size class does not meet the condition. It cannot be stated categorically that the two larger size classes feed only once a day but it has already been shown in chapter 1 that mean fullness index increases throughout the night and few eels are caught during the daylight hours, so feeding is restricted to one, albeit rather long, interval.

2. It has been established in this chapter that evacuation times for invertebrates are short, usually less than 12 hours. Fish prey take 33 hours to be evacuated and, therefore, could overlap the next feeding period.

This chapter gives results for gastric evacuation times, so that condition 3. is also met.

The equation (from Davis and Warren, 1971) is;

$$r = S/Vn$$

where r = mean daily ration as a percentage of body weight.
S = reconstructed total weight of food eaten by all the fish in the sample expressed as a percentage of body weight.
V = number of days taken to digest a meal.
n = total number of fish in the sample.

This equation has been modified to suit the present study by using calorific values (joules) instead of weights and not expressing as a percentage of body weight.

Several assumptions with respect to V are required to take this equation further:

i) The gastric evacuation experiments show that invertebrates are evacuated in under 12 hours at 20°C. Evacuation time at autumn and spring temperatures is likely to be about 18 hours (assuming a $Q_{10}$ of 2). For the invertebrate part of the diet V is, therefore, assumed to be 1.

ii) The gastric evacuation experiments show that total evacuation of bullies from eel stomachs occurs 33 hours after ingestion at 20°C. The figure of 1.5 for V was, therefore, adopted for eels ingesting fish in summer. Eels ingesting fish in spring and autumn were assumed to have a V value of two, which corrects for the slower evacuation rates induced by lower temperatures.

Neither of these assumptions takes into account slower evacuation rate of prey larger than the size range for which the gastric evacuation experiments were conducted. (Evacuation rate increases as the size of prey increases but must eventually asymptote. Increasing the ration above this size will not further increase rate. It is not known what ration size will produce the asymptote.)

Choice of V can markedly affect the calculated daily ration so it is important to choose a value with care. The values assumed in this study are an approximation based upon limited experimentation. Further gastric evacuation experiments would enable values of V to be fixed more accurately. However, as no work of this nature has been published for *A. a. schmidtii*, the results based on these assumptions will provide a starting point for further study.

The equation was applied (using calorific values from Tables A.1-A.16) to seasonal data, so r is the mean seasonal daily ration for the size class under consideration. Winter was not included as the sample size was so small. For the purpose of this analysis it was assumed that eels do not feed in winter - an assumption supported by several authors (see chapter 1). This point has been discussed at some length in chapter 1. To obtain the mean annual daily ration, the mean figure for spring, summer, and autumn was first calculated. Winter was assumed to be zero. The results are given in Table 38.

Table 38. Seasonal and annual mean daily ration for 40.1-50 cm and >50.1 cm size class eels.

| | Size class | |
|---|---|---|
| Season | 40.1-50 cm | >50.1 cm |
| Spring | 1551 j | 5843 j |
| Summer | 1525 j | 3838 j |
| Autumn | 550 j | 3368 j |
| Year | 906 j | 3262 j |

Gross annual calorific input was attained by multiplying annual daily ration by 365 which gave 330 909 j for 40.1-50 cm eels and 1 190 703 j for >50.1 cm eels. The mean size of the 40.1-50 cm size class eel was 44.78 cm and for the >50.1 cm size class eel was 57.04 cm.

Growth of eels in calorific terms

To investigate growth of a representative individual of each size class, the age at which the mean length is obtained was derived from Tables A.19-20. The 40.1-50 cm size class contains both male and female fish, so the growth rate for all fish was used. The >50.1 cm size class is almost all female, so the female growth rate was used. The length of age class 17 eels, from the table of growth of all fish (Table A.19), coincides almost exactly with the mean length of 40.1-50 cm fish. Mean length of age class 17 fish was 44.80 cm compared with 44.78 cm from Table A.19. Interpolated mean size of age class 16 1/2 was 44.23 cm and for age class 17 1/2, 45.47 cm. For female fish the agreement was not quite as good, the mean size was

57.03 cm compared with 56.94 cm for age class 28 fish. Size of age class 27 1/2 fish, by interpolation, was 56.62 cm and for age class 28 1/2 was 57.59 cm.

Replacing these interpolated lengths in the equation describing length and weight (page 33, chapter 1) gives weights, for the 40.1-50 cm eels of age class 16 1/2 = 158.50 g and of age class 17 1/2 = 171.40 g; and for >50.1 cm eels of age class 27 1/2 = 334.80 g and of age class 28 1/2 = 353.60 g. These results should be multiplied by 1.0280, the mean condition factor for autumn eels (see page 34, chapter 1). (The regression used to obtain the length/weight relationship gives the mean weight of any particular length fish. The condition factor for the average fish is 1.0000. As condition factor increases as a result of increasing weight only, multiplying by 1.0280 changes the calculated weight from that of the mean fish to that of the mean fish in autumn.) Multiplying by this factor gives a mean increment in weight for the 40.1-50 cm size class of 13.26 g and for the >50.1 cm class of 19.32 g. These results are for wet weight only. To obtain dry weight, wet weight of the 40.1-50 cm fish should be multiplied by 0.2802 (mean of 8 samples) and of the >50.1 cm fish by 0.3163 (mean of 3 samples). Mean increment in dry weight for the 40.1-50 cm fish was, therefore, 3.7154 g and for the bigger size class - 6.1109 g. Using the mean calorific value for each size class (from page 91 chapter 2) gives an annual increment for the 40.1-50 cm size class of 85 857 j and for the >50.1 cm fish of 173 944 j.

Ivlev's energy coefficient of the first order

It is now possible to apply Ivlev's energy coefficient of the first order. The coefficient is (Davis and Warren, *loc. cit.*);

$$K = \Delta B/C$$

where $\Delta B$ is growth per unit time.

C is total energy input.

For the 40.1-50 cm fish,

$$K = 85\ 857/330\ 909$$
$$= 0.259$$

and for >50.1 cm fish,

$$K = 173\,944/1\,190\,703$$
$$= 0.146$$

These results compare favourably with those in the literature. Kelso (1972) found K values of 0.143 and 0.136 at 20°C and 12°C respectively for walleye (*Stizostedion vitreum vitreum*). Swenson and Smith (1973) found conversion efficiencies of between 0.169 and 0.609 with a mean of about 0.230 also for walleye. Swenson and Smith did not determine the calorific values of ΔB and C but expressed efficiency solely in terms of weight. Wissing (1974) found values of K between 0.173 and 0.353 for young-of-the-year white bass (*Morone chrysops*). Pierce and Wissing (1974) found K values of between 0.30 and 0.44 for the bluegill sunfish (*Lepomis macrochirus*), but Kohlenmainen (1974) (using a radio-isotope method) found a K value of only 0.04. Jezierska (1975) found different values in perch (*Perca fluviatilis*) fed on different food species. Values ranged from 0.12 to around 0.200. Elliott (1976) determined K values for brown trout (*Salmo trutta*) fed at different temperatures and obtained values from 0.03 to 0.34. Mironova (1976) found that assimilation efficiency in *Tilapia mossambica* increased as the fish grew. Reddy *et al.* (1977) found a K value of approximately 0.05 for elvers of *A. nebulosa* fed on *Tubifex*. This result was determined using wet weights not calorific values. Such a low efficiency may explain the apparent slow growth rates of elvers in the study by Pantulu and Singh (1962). The results for *A. a. schmidtii*, while based on assumptions that may not be entirely valid, are quite feasible and agree well with the general values given in the literature. The only other results for *A. a. schmidtii* available for comparison with the present study are those obtained by Crossland (1972). He found values for *A. a. schmidtii* ranging between 0.185 and 0.252 for fish fed in aquaria. His range is only slightly smaller than the figures for wild fish presented here.

Ivlev's energy coefficient of the second order

While gross ecological efficiency (K) is useful, it gives no information on the fate of the energy ingested that is not

used in growth. Therefore, assimilation efficiency experiments were set up to determine Ivlev's energy coefficient of the second order. This coefficient is the ratio of growth increment to food consumed less waste products.

$$K_2 = \Delta B/C - (F + U)$$

where F is energy value of faeces and U is soluble wastes.

Soluble wastes were ignored because they were too difficult to collect. Winberg (1956) suggests that soluble losses constitute no more than 3% of the energy value of the food consumed, although Elliott (1976) questions this assumption. It was accepted in this study that any assimilation efficiency determined must represent a maximum. Results for assimilation experiments are presented in Tables 39, 40 and 41. These results represent the upper limit in assimilation efficiency; as has already been pointed out, soluble losses were ignored. The small standard error for each set of results indicates that the method used was basically sound. The high figure for eels fed on *G. cotidianus* does have parallels in the literature. Kelso (1972) found assimilation efficiencies of 82.1-97.9% for walleye (*Stizostedion vitreum vitreum*) fed on fish. Assimilation efficiency decreased with increasing walleye size. Wissing (1974) in his study on young-of-the-year white bass, found

Table 39. Percentage assimilation of *A. annectens* fed to *A. a. schmidtii* (based upon calorific value). The mean ($\bar{Y}$) ± the standard error of the mean ($S\bar{Y}$) is also given.

| Eel weight (g) | % assimilation |
|---|---|
| 227 | 70.0 |
| 147 | 75.0 |
| 297 | 71.0 |
| 134 | 62.0 |
| 184 | 69.5 |
| 303 | 63.7 |
| 126 | 65.3 |

$\bar{Y} = 68.07 \pm 1.6$

assimilation efficiencies of 67% for fish feeding naturally on cladocerans, copepods, amphipods, and insect larvae and pupae. These results are very similar to the 68% for eels fed on *A. annectens* in the present study. Assimilation efficiency of trout (*Salmo gairdneri*) varies from 52-95%, depending upon diet (Halver, 1972, Brocksen and Bugge, 1974). Staples and Nomura (1976) found that the assimilation efficiency of trout was independent of body size and food ration.

These results can now be used to determine $K_2$. The assumptions underlying this calculation are that assimilation efficiency is similar for all fish in the size range examined (>40.1 cm) and that it does not vary with temperature. The first assumption is reasonable and is supported by Staples and Nomura (*loc. cit.*), the second is more difficult to justify. In general, assimilation efficiency increases with temperature (Mironova, 1976). All experiments were conducted at 20°C (the highest temperature likely to be encountered in Lake Ellesmere (see Fig. 2, chapter 1). Assimilation efficiency at this temperature should, therefore, be higher than the efficiencies of most eels in the lake. This suggestion does not support the assumption that assimilation efficiencies do not vary with temperature but it does suggest that assimilation experiments conducted at 20°C will tend to give maximum assimilation efficiencies. It has already been pointed out that the figures obtained are maximum figures because of ignoring the soluble losses. These two factors ensure that figures obtained for assimilation efficiencies will be higher than those exhibited by eels in Lake Ellesmere.

No figures for assimilation efficiency were available for prey organisms other than those presented. The figure for *A. annectens* was used for all invertebrates other than *P. antipodarum*. Little bias is introduced by this procedure as the total contribution of invertebrates other than *P. antipodarum* to the diet of the two size classes under consideration is small. The value for *G. cotidianus* was used for all fish. The mean assimilable daily ration is given in Table 42.

Table 40. Percentage assimilation of *P. antipodarum* fed to *A. a. schmidtii* (based upon calorific value). The mean ($\bar{Y}$) ± the standard error of the mean ($S\bar{Y}$) is also given.

| Eel weight (g) | % assimilation |
|---|---|
| 371 | 48.2 |
| 377 | 41.8 |
| 300 | 44.8 |
| 245 | 45.9 |
| 137 | 49.5 |
| 368 | 40.3 |
| 335 | 42.1 |

$\bar{Y} = 44.6 \pm 1.20$

Table 41. Percentage assimilation of *G. cotidianus* fed to *A. a. schmidtii* (based on calorific value). The mean ($\bar{Y}$) ± standard error of the mean ($S\bar{Y}$) is also given.

| Eel weight (g) | % assimilation |
|---|---|
| 240 | 91.8 |
| 143 | 97.7 |
| 380 | 98.7 |
| 295 | 98.4 |
| 425 | 97.5 |
| 380 | 98.1 |
| 210 | 95.0 |

$\bar{Y} = 96.7 \pm 0.87$

Table 42. Mean assimilable daily ration (joules)

| Season | 40.1-50 cm | >50.1 cm |
|---|---|---|
| Spring | 1320 | 5169 |
| Summer | 976 | 1725 |
| Autumn | 570 | 3085 |
| Year | 716 | 2495 |

Mean annual assimilable ration for 40.1-50 cm fish is, therefore, 261 632 j and for >50.1 cm fish is 910 675. For 40.1-50 cm fish,

$$K_2 = 85\ 857/261\ 632$$
$$= 0.328$$

and for >50.1 cm fish,

$$K_2 = 0.191$$

These results are similar to those reported by Kelso (*loc. cit.*) for walleye of 0.117-0.149. Wissing (*loc. cit.*) gives values of between 0.25 and 0.53 for white bass. Jezierska (1975) found values for perch of 0.30.

Metabolism

The amount of energy not used in growth and not egested in faeces is presumably used in metabolism. According to Winberg's balanced equation (Warren and Davis, 1967);

$$C = F + U + \Delta B + R$$

where C = energy value of food consumed.
F = energy value of faeces.
U = energy value of materials excreted in the urine or through the gills or skin.
$\Delta B$ = total change in the energy value of materials of body (growth).
R = total energy of metabolism.

In this study C, F and ΔB are known. As U has been ignored, the equation for calculation for $K_2$ becomes;

$$K_2 = \Delta B/(C - F)$$

which transforms to

$$F = C - \Delta B/K_2.$$

If this value is inserted into the balanced equation, it becomes;

$$C = C - \Delta B/K_2 + \Delta B + R$$

or $$R = \Delta B/K_2 - \Delta B$$

Therefore, R (annual figure) can be calculated for an average eel of each size class.
For 40.1-50 cm fish,

$$R = 85\ 857/0.328 - 85\ 857\ j$$
$$R = 175\ 902.7\ j$$

and for >50.1 cm fish,

$$R = 173\ 944/0.191 - 173\ 944$$
$$R = 736\ 757.5\ j$$

This computation gives a daily expenditure of 481.9 j for the smaller fish and 2018.5 j for fish longer than 50.1 cm. Expressed as a percentage of the total daily energy ingested;
For 40.1-50 cm fish,

Energy expenditure = 53.1% of energy ingested

and for the >50.1 cm fish,

Energy expenditure = 61.8% of energy ingested

These values are for routine metabolism-activity of fish in the field. Expressing the balanced equation in percentages, we

get for 40.1-50 cm size class fish;

$$C(100) = F(21) + \Delta B(25.9) + R(53.1)$$

and for >50.1 cm fish,

$$C(100) = F(23.6) + \Delta B(14.6) + R(61.8)$$

These results suggest that the assimilation efficiencies are similar for the two size classes but the 40.1-50 cm fish put more energy into growth and less into respiration than do the larger size class.

The metabolism figures can be converted to oxygen consumed by dividing the number of joules used in metabolism by the oxycalorific coefficient of 14.319 j/mg $O_2$.
Which gives, for 40.1-50 cm size,

1.40 mg $O_2$/hour for a mean eel of weight 165 g

and for >50.1 cm fish,

5.8 mg $O_2$/hour for a mean eel weight of 334 g.

The only figures for species other than *A. a. schmidtii* available for comparison are those given by Nicol (1960) and Precht (1961) quoted in Jedryczkowski and Fischer (1973) for feeding *A. anguilla*. These results were expressed in $\ell$ $O_2$/hour/individual. Transformed into mg $O_2$/hour they give a mean figure of 4.2 mg $O_2$/hour which falls within the range found in the present study. The only results available for *A. a. schmidtii* are those given by Crossland (1972). He found consumption rates of approximately 27 mg $O_2$/hour (at 20°C) for a 349 g eel and 16 mg $O_2$/hour (at 18°C) for a 159 g individual.

All available results are compared in Table 43.

The figures for calorific cost of metabolism in the eel are comparable with values given by Kelso (*loc. cit.*) of 82.8% for walleye at 20°C. Mironova (*loc. cit.*) gives values ranging from 15.9% to 75.5% in *Tilapia mossambica* kept at varying temperatures and fed different rations. The close agreement of my results with the figure given by Nicol (*loc. cit.*) and Precht

Table 43. Oxygen consumption found for *Anguilla* sp. in different studies.

| Species | Author | Eel size (g) | $O_2$ consumption (mg $O_2$/ individual/hour) | (mg $O_2$/Kg/ hour) | Water temp. (°C) |
|---|---|---|---|---|---|
| *A. a. schmidtii* | Ryan (this study) | 165 | 1.4 | | 12.1 |
| | | 334 | 5.8 | | 12.1 |
| *A. a. schmidtii* | Crossland (1972) | 159 | 16 | 100 | 19 |
| | | 349 | 27 | 75.6 | 16 |
| *A. anguilla* | Nicol (1960) Precht (1961) | ? | 4.2 | ? | ? |

(*loc. cit.*) gives support to the assumptions that were made in the course of this study. It is pleasing that one method, by direct measurement, and the other, by indirect measurement, give similar results.

The figures given by Crossland were obtained using a closed bottle technique and the eels were presumably under considerable stress. His results are higher than mine by a large factor, but this may be due to his experimental technique.

SUMMARY

It was established by experimentation that the gastric evacuation time of eels fed *G. cotidianus* at a ration level of approximately 1 mg dry weight of *G. cotidianus*/g wet weight of eel, was 33 hours at 20°C. Force-fed eels exhibited an identical evacuation rate but with a longer time lag. The difference in time for the onset of evacuation between the two experiments was assumed to be due to the effects of force-feeding. The difference of 5.1 hours was used also in subsequent experiments with the isopod, *A. annectens*, which was fed to eels at ration levels of 0.2, 0.4, and 0.8 mg. Total evacuation times were similar for all three ration levels, but there was a varying lag time before the onset of evacuation. The reason for this time lag is not known but may be due to force-feeding. Net evacuation times were plotted against ration level and a predictive regression equation for evacuation time with respect to ration size determined.

To determine the effect of food species on evacuation rate, an experiment was carried out with *P. antipodarum* fed at a ration level of 0.8 mg/g wet weight of eel at 20°C to compare with the isopod result. While gross evacuation time was similar to the isopod figure, the rate was much slower. It was concluded that gastric evacuation rate may be food species specific.

The results obtained in the gastric evacuation experiments enabled a modified form of Fortunatova's (1950) formula to be used to obtain daily ration. The formula was applied to the 40.1-50 cm and >50.1 cm size classes only, as it was considered that the ⩽40 cm size class did not meet with the necessary assumptions. These results were used in conjunction with growth rate results (from chapter 2) to calculate K values, and gave 0.259 for 40.1-50 cm eels and 0.146 for the >50.1 cm eels. These values are similar to values reported for other fish species.

Assimilation experiments were carried out using *A. annectens*, *P. antipodarum* and *G. cotidianus* as prey species. All experiments were carried out at a ration level of 0.8 mg/g wet weight of eel and at a temperature of 20°C. Results for *A. annectens* showed a percentage assimilability of 68%, for *P. antipodarum*

44.6% and for *G. cotidianus* 96.7%. Comparable results are given in the literature. These assimilation results were used in conjunction with the results from the calorific value of prey species tables (A.1-A.16) and with values of K, to calculate $K_2$ values. These were 0.328 for 40.1-50 cm fish and 0.191 for >50.1 cm fish. Results given in the literature for other fish species are comparable.

The total energy of metabolism for each size class was then determined from Winberg's balanced equation using the $K_2$ values and the daily energy budget was presented for both size classes. It is believed to be the first time such a result has been obtained for *A. a. schmidtii* by utilising field data. The hourly $O_2$ consumption for both size classes was determined by applying the oxycalorific coefficient which gave hourly $O_2$ consumption levels (routine metabolism) of 1.4 mg for the 40.1-50 cm fish and 5.8 mg for the >50.1 cm eels. The only comparable results obtained by respirometry experiments on *A. anguilla* and *A. a. schmidtii* give similar results to those obtained in the present study.

## CONCLUSION

Most of the approaches used in this study have not previously been employed in studies of eel biology and many of the findings are, therefore, new. Gastric evacuation experiments have been conducted on other fish species, but the only reported attempt for a species of *Anguilla* was by Sinha and Jones (1975) and was unsuccessful. The results obtained from the gastric evacuation experiments in this study are important as they provide the basis for the development of a model for daily ration, which has not previously been determined for wild eels. The assimilation experiments utilising natural prey organisms were also new and enabled a daily energy budget to be calculated. Although neither of these kinds of experiment has previously been reported for the eel, the values obtained fit well within the range reported for other species of fish. Results from feeding *Austridotea annectens* to experimental eels at different ration levels showed that evacuation rates were faster at the higher ration level. This result supports work by Seaburg and Moyle (1964), Windell (1966), Tyler (1970), Elliott (1972), Swenson and Smith (1973), Steigenburger and Larkin (1974) and Jobling *et al.* (1977).

The more traditional aspects of this study have also revealed some new information on eel biology. While it has always been tacitly assumed, this study is the first to show conclusively that eels are nocturnal feeders. Activity changed with season, reaching a peak in spring and, as in other studies, was shown to be minimal in winter.

It was also found that the relative importance of any prey species in the eel diet depended to a large extent on the analysis method chosen. A new analysis method combining both the predicted and actual dry weight of prey organisms was used successfully and it is suggested that this method could be useful in other fish studies. The importance of prey species was also expressed calorifically to enable the daily ration to be determined in energetic terms. No published eel research has employed this method in food analyses. From these results it was possible to show that eel diet changes with size. Small eels $\leq$40 cm fed almost entirely on invertebrates. The 40.1-50 cm eels fed on both invertebrates and fish. Eels

>50.1 cm were almost entirely piscivorous. Hartley (1940) and Moriarty (1972) are the only European workers to demonstrate a change in diet as eels grow.

Growth rates, obtained from back calculation of otolith data, showed that Lake Ellesmere *A. a. schmidtii* grew faster in their first three years in freshwater than do other *Anguilla* species. Growth rates from age class three onwards was extremely slow. Selwyn River female eels exhibited faster growth rates than lake females, so it was concluded that interchange between populations was small. Analysis of the growth rates showed that increased fishing pressure resulted in faster eel growth, probably due to decreased intra-specific competition. Annual increases in calorific value for the average 40.1-50 cm and >50.1 cm eels were calculated. These results, together with information on daily ration, enabled K values to be obtained which were similar to those recorded in the literature for other fish species (Kelso, 1972, Swenson and Smith, 1973, Wissing, 1974, Pierce and Wissing, 1974, Kohlenmainen, 1974, Jezierska, 1975, Elliott, 1976 and Mironova, 1976). Values for *A. a. schmidtii* given by Crossland (1972) were also similar. Results from the assimilation experiments enabled $K_2$ values to be determined and hence the daily energy budget and $O_2$ consumption could be calculated from the balanced equation. $O_2$ consumption rates were similar to those given by Nicol (1960) and Precht (1961, in Jedryczkowski and Fischer, 1973) for *A. anguilla* and by Crossland (1972) for *A. a. schmidtii*. As far as is known, this study is the first to determine routine metabolism of wild eels.

The work presented here has filled in several gaps in our knowledge of *A. a. schmidtii*, and of *Anguilla* sp. in general. Most of the research is new and has helped lay the foundation for future avenues of work. The biggest gap in the knowledge of the feeding of *Anguilla* species is in the food habits of the small (<30 cm) eels. Energetics orientated research on this topic would be useful. Several observations in this study have suggested that comprehensive gastric evacuation models cannot be determined. Further information on gastric evacuation rates with respect to temperature and ration size would, however, be extremely useful.

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APPENDIX

Table A.1. Estimated calorific values and dry weights of food species from stomachs of eels ≤40 cm captured in spring. Percentage of total in brackets.

| Prey organism | Dry weight (g) | | Calorific value (joules) | |
|---|---|---|---|---|
| *T. chiltoni* | 0.0162 | (1.0) | 343.3 | (2.1) |
| *P. fluviatilis* | 0.1286 | (9.0) | 2 259.3 | (13.4) |
| *A. annectens* | 0.2809 | (19.6) | 3 418.7 | (20.3) |
| *C. zealandicus* larvae | 0.0971 | (6.8) | 1 707.9 | (10.1) |
| *P. antipodarum* | 0.6447 | (45.1) | 3 416.6 | (20.3) |
| *G. maculatus* | 0.1075 | (7.5) | 2 250.5 | (13.3) |
| Other | 0.1543 | (10.8) | 3 412.2 | (20.3) |
| | 1.4293 | | 16 808.5 | |

Table A.2. Estimated calorific values and dry weights of food species from stomachs of 40.1-50 cm eels captured in spring. Percentage of total in brackets.

| Prey organism | Dry weight (g) | | Calorific value (joules) | |
|---|---|---|---|---|
| *T. chiltoni* | 0.0663 | (0.5) | 1 325.2 | (0.6) |
| *P. fluviatilis* | 0.1091 | (0.8) | 1 916.8 | (0.9) |
| *A. annectens* | 0.4057 | (3.1) | 5 224.1 | (2.5) |
| *P. antipodarum* | 3.8128 | (29.1) | 20 699.7 | (9.8) |
| *R. retropinna* | 3.8130 | (29.1) | 79 207.4 | (38.0) |
| *G. cotidianus* | 4.7334 | (36.2) | 98 298.2 | (46.8) |
| Other | 0.1503 | (1.1) | 2 785.6 | (1.3) |
| | 13.0906 | | 209 456.7 | |

Table A.3. Estimated calorific values and dry weights of food species from stomachs of spring eels longer than 50 cm. Percentage of total in brackets.

| Prey organism | Dry weight (g) | | Calorific value (joules) | |
|---|---|---|---|---|
| *T. chiltoni* | 0.2742 | (0.7) | 5 865.6 | (0.8) |
| *P. fluviatilis* | 0.2456 | (0.6) | 4 314.7 | (0.6) |
| *A. annectens* | 0.7931 | (2.0) | 9 100.9 | (1.3) |
| *P. antipodarum* | 9.2916 | (23.6) | 46 430.5 | (6.7) |
| *G. maculatus* | 0.1491 | (0.4) | 3 297.2 | (0.4) |
| *R. retropinna* | 15.2500 | (38.8) | 316 788.2 | (46.0) |
| *G. cotidianus* | 13.3164 | (33.8) | 305 244.9 | (44.0) |
| Other | 0.0134 | (0.03) | 323.2 | (0.04) |
| | 39.3334 | | 691 365.2 | |

Table A.4. Estimated calorific values and dry weights of food species from stomachs of all spring eels. Percentage of total in brackets.

| Prey organism | Dry weight (g) | | Calorific value (joules) | |
|---|---|---|---|---|
| *T. chiltoni* | 0.3567 | (0.7) | 7 534.1 | (0.8) |
| *P. fluviatilis* | 0.4833 | (0.9) | 8 490.8 | (0.9) |
| *A. annectens* | 1.4797 | (2.7) | 17 743.7 | (2.0) |
| *C. zealandicus* larvae | 0.1028 | (0.2) | 1 807.9 | (0.2) |
| *P. antipodarum* | 13.7491 | (25.5) | 70 546.8 | (7.7) |
| *G. maculatus* | 0.2566 | (0.5) | 5 674.4 | (0.6) |
| *R. retropinna* | 19.0630 | (35.4) | 395 995.7 | (43.3) |
| *G. cotidianus* | 18.0498 | (33.5) | 403 543.0 | (43.8) |
| Other | 0.3123 | (0.6) | 5 891.5 | (0.6) |
| | 53.8533 | | 917 227.9 | |

Table A.5. Estimated calorific values and dry weights of food species from stomachs of ⩽40 cm summer eels. Percentage of total in brackets.

| Prey organism | Dry weight (g) | | Calorific value (joules) | |
|---|---|---|---|---|
| Oligochaeta | 0.4115 | (9.2) | 8 614.7 | (11.3) |
| *T. chiltoni* | 0.1235 | (2.8) | 2 449.8 | (3.2) |
| *A. annectens* | 0.2304 | (5.2) | 3 337.9 | (4.4) |
| *C. zealandicus* larvae | 1.5576 | (34.9) | 27 397.6 | (36.1) |
| *C. zealandicus* pupae | 0.0974 | (2.2) | 1 713.3 | (2.3) |
| *P. antipodarum* | 0.6190 | (13.8) | 2 978.6 | (3.9) |
| *R. retropinna* | 1.2500 | (28.0) | 25 966.2 | (34.5) |
| Other | 0.1741 | (3.9) | 3 189.2 | (4.2) |
| | 4.4635 | | 75 647.3 | |

Table A.6. Estimated calorific values and dry weights of food species from stomachs of 40.1-50 cm summer eels. Percentage of total in brackets.

| Prey organism | Dry weight (g) | | Calorific value (joules) | |
|---|---|---|---|---|
| Oligochaeta | 0.5200 | (8.3) | 10 886.2 | (13.3) |
| *A. annectens* | 0.0373 | (0.6) | 512.5 | (0.6) |
| *C. zealandicus* larvae | 2.7737 | (44.2) | 48 788.2 | (59.8) |
| *C. zealandicus* pupae | 0.0854 | (1.4) | 1 501.9 | (1.8) |
| *P. antipodarum* | 2.0832 | (33.2) | 9 928.4 | (12.2) |
| *G. cotidianus* | 0.3260 | (5.2) | 6 732.7 | (8.3) |
| Other | 0.4384 | (7.0) | 3 208.5 | (3.4) |
| | 6.2640 | | 81 558.4 | |

Table A.7. Estimated calorific values and dry weights of food species from stomachs of eels >50.1 cm caught in summer. Percentage of total in brackets.

| Prey organism | Dry weight (g) | | Calorific value (joules) | |
|---|---|---|---|---|
| *P. antipodarum* | 6.6535 | (39.2) | 32 235.3 | (12.9) |
| *G. maculatus* | 2.6000 | (15.3) | 57 496.4 | (23.0) |
| *R. retropinna* | 1.2000 | (7.1) | 25 122.0 | (10.0) |
| *C. carassius auratus* | 0.2069 | (1.2) | 4 331.4 | (1.7) |
| *G. cotidianus* | 6.1385 | (36.2) | 128 536.7 | (51.4) |
| Other | 0.1520 | (0.9) | 2 705.6 | (1.1) |
| | 16.9509 | | 250 133.4 | |

Table A.8. Estimated calorific values and dry weights of food species from stomachs of all summer eels. Percentage of total in brackets.

| Prey organism | Dry weight (g) | | Calorific value (joules) | |
|---|---|---|---|---|
| Oligochaeta | 0.9315 | (3.4) | 19 500.9 | (4.8) |
| *T. chiltoni* | 0.1414 | (0.5) | 3 002.5 | (0.7) |
| *A. annectens* | 0.3002 | (1.1) | 4 298.4 | (1.1) |
| *C. zealandicus* | 4.4213 | (16.0) | 77 769.7 | (19.1) |
| *C. zealandicus* | 0.1828 | (0.7) | 3 215.2 | (0.8) |
| *P. antipodarum* | 9.3557 | (34.0) | 45 142.1 | (11.1) |
| *G. maculatus* | 2.6000 | (9.5) | 57 496.4 | (14.1) |
| *R. retropinna* | 2.4500 | (8.8) | 50 893.8 | (12.5) |
| *C. carassius auratus* | 0.2069 | (0.8) | 4 331.4 | (1.0) |
| *G. cotidianus* | 6.4645 | (23.4) | 135 269.4 | (33.2) |
| Other | 0.6241 | (2.2) | 6 520.0 | (1.6) |
| | 27.6784 | | 407 493.8 | |

Table A.9. Estimated calorific values and dry weights of food species from stomachs of autumn eels ⩽40 cm. Percentage of total in brackets.

| Prey organism | Dry weight (g) | | Calorific value (joules) | |
|---|---|---|---|---|
| *T. chiltoni* | 0.0916 | (11.4) | 1 825.1 | (12.5) |
| *A. annectens* | 0.1539 | (19.2) | 2 190.2 | (12.6) |
| *C. zealandicus* larvae | 0.1765 | (22.1) | 3 105.1 | (21.3) |
| *Costelytra* sp. | 0.0945 | (11.8) | 1 976.3 | (13.6) |
| *P. antipodarum* | 0.0137 | (1.7) | 56.5 | (0.4) |
| *G. cotidianus* | 0.2445 | (30.6) | 5 313.3 | (36.5) |
| Other | 0.0233 | (2.9) | 450.1 | (3.0) |
| | 0.7980 | | 14 916.6 | |

Table A.10. Estimated calorific values and dry weights of food species from stomachs of 40.1-50 cm autumn eels. Percentage of total in brackets.

| Prey organism | Dry weight (g) | | Calorific value (joules) | |
|---|---|---|---|---|
| *T. chiltoni* | 0.3880 | (19.6) | 7 766.5 | (20.3) |
| *A. annectens* | 0.0065 | (0.3) | 123.5 | (0.3) |
| *C. zealandicus* larvae | 0.6610 | (33.3) | 11 626.5 | (30.3) |
| *P. antipodarum* | 0.0373 | (1.9) | 152.8 | (0.4) |
| *G. maculatus* | 0.1700 | (8.6) | 3 759.4 | (9.8) |
| *G. cotidianus* | 0.6254 | (31.5) | 13 377.5 | (34.8) |
| Other | 0.0938 | (4.7) | 1 601.9 | (4.2) |
| | 1.9820 | | 38 408.1 | |

Table A.11. Estimated calorific values and dry weights of food species from stomachs of autumn eels longer than 50.1 cm. Percentage of total in brackets.

| Prey organism | Dry weight (g) | | Calorific value (joules) | |
|---|---|---|---|---|
| *T. chiltoni* | 0.3625 | (2.0) | 7 261.5 | (2.2) |
| *C. zealandicus* larvae | 0.0526 | (0.3) | 924.9 | (0.3) |
| *P. antipodarum* | 3.0747 | (17.5) | 12 186.9 | (3.8) |
| *G. maculatus* | 0.7489 | (4.3) | 16 561.1 | (4.8) |
| *R. retropinna* | 6.2100 | (35.3) | 129 000.3 | (40.2) |
| *C. carassius auratus* | 0.5400 | (3.0) | 11 304.0 | (3.5) |
| *G. cotidianus* | 6.5690 | (37.3) | 145 435.4 | (45.0) |
| Other | 0.0249 | (0.15) | 195.9 | (0.1) |
| | 17.5826 | | 322 870.0 | |

Table A.12. Estimated calorific values and dry weights of food species from stomachs of all autumn eels. Percentage of total in brackets.

| Prey organism | Dry weight (g) | | Calorific value (joules) | |
|---|---|---|---|---|
| *T. chiltoni* | 0.8421 | (4.1) | 16 853.1 | (4.5) |
| *A. annectens* | 0.1604 | (0.8) | 2 313.7 | (0.6) |
| *C. zealandicus* larvae | 0.8901 | (4.3) | 15 656.4 | (4.1) |
| *P. antipodarum* | 3.1257 | (15.4) | 12 396.2 | (3.3) |
| *G. maculatus* | 0.9189 | (4.5) | 20 320.5 | (5.4) |
| *R. retropinna* | 6.2100 | (30.5) | 129 000.3 | (34.2) |
| *C. carassius auratus* | 0.5400 | (2.7) | 11 304.9 | (3.0) |
| *G. cotidianus* | 7.4389 | (36.5) | 164 126.2 | (43.7) |
| Other | 0.2365 | (1.2) | 4 224.3 | (1.1) |
| | 20.3626 | | 376 195.6 | |

Table A.13. Estimated calorific values and dry weights of food species from stomachs of all ⩽40 cm eels. Percentage of total in brackets.

| Prey organism | Dry weight (g) | | Calorific value (joules) | |
|---|---|---|---|---|
| Oligochaeta | 0.4715 | (6.9) | 9 870.8 | (9.0) |
| *T. chiltoni* | 0.2313 | (3.4) | 4 618.3 | (4.2) |
| *P. fluviatilis* | 0.1286 | (1.9) | 2 259.3 | (2.1) |
| *A. annectens* | 0.6904 | (10.1) | 9 288.0 | (8.5) |
| *C. zealandicus* | 1.8312 | (26.9) | 32 209.7 | (29.4) |
| *C. zealandicus* | 0.0974 | (1.4) | 1 713.3 | (1.6) |
| *Costelytra* | 0.1360 | (2.0) | 2 755.0 | (2.5) |
| *P. antipodarum* | 1.2774 | (18.7) | 6 451.7 | (5.9) |
| *G. maculatus* | 0.1075 | (1.6) | 2 377.2 | (2.2) |
| *R. retropinna* | 1.2500 | (18.3) | 25 966.2 | (23.7) |
| *G. cotidianus* | 0.2445 | (3.6) | 5 313.3 | (4.9) |
| Other | 0.3517 | (5.2) | 6 521.2 | (6.0) |
| | 6.8175 | | 109 340.0 | |

Table A.14. Estimated calorific values and dry weights of food species from stomachs of all 40.1-50 cm eels. Percentage of total in brackets.

| Prey organism | Dry weight (g) | | Calorific value (joules) | |
|---|---|---|---|---|
| Oligochaeta | 0.5200 | (2.4) | 10 886.2 | (3.3) |
| *T. chiltoni* | 0.4543 | (2.1) | 9 091.6 | (2.8) |
| *P. fluviatilis* | 0.1091 | (0.5) | 1 916.8 | (0.6) |
| *A. annectens* | 0.4495 | (2.1) | 5 860.1 | (1.8) |
| *C. zealandicus* larvae | 3.4347 | (16.1) | 60 415.0 | (18.3) |
| *C. zealandicus* pupae | 0.0854 | (0.4) | 1 501.9 | (0.5) |
| *P. antipodarum* | 5.9333 | (27.8) | 30 780.7 | (9.3) |
| *G. maculatus* | 0.1700 | (0.8) | 3 759.4 | (1.1) |
| *R. retropinna* | 3.8130 | (17.9) | 79 207.4 | (24.0) |
| *G. cotidianus* | 5.6848 | (26.7) | 118 408.4 | (35.9) |
| Other | 0.6825 | (3.2) | 7 596.0 | (2.3) |
| | 21.3366 | | 329 423.5 | |

Table A.15. Estimated calorific values and dry weights of food species from stomachs of all eels longer than 50.1 cm. Percentage of total in brackets.

| Prey organism | Dry weight (g) | | Calorific value (joules) | |
|---|---|---|---|---|
| *T. chiltoni* | 0.6533 | (0.8) | 13 472.5 | (1.0) |
| *A. annectens* | 0.8276 | (1.0) | 9 583.2 | (0.7) |
| *P. antipodarum* | 19.0300 | (23.8) | 90 890.5 | (6.5) |
| *G. maculatus* | 3.4980 | (4.4) | 77 354.8 | (5.5) |
| *R. retropinna* | 22.6600 | (28.4) | 470 716.2 | (33.7) |
| *C. carassius auratus* | 0.7469 | (0.9) | 15 636.3 | (1.1) |
| *G. cotidianus* | 31.8969 | (40.0) | 706 321.8 | (50.7) |
| Other | 0.5539 | (0.7) | 9 702.9 | (0.7) |
| | 79.8666 | | 1 393 678.2 | |

Table A.16. Estimated calorific values and dry weights of food species from stomachs of all eels captured. Percentage of total in brackets.

| Prey organism | Dry weight (g) | | Calorific value (joules) | |
|---|---|---|---|---|
| Oligochaeta | 0.9915 | (0.9) | 20 757.0 | (1.1) |
| *T. chiltoni* | 1.3568 | (1.3) | 27 735.1 | (1.5) |
| *A. annectens* | 1.9856 | (1.8) | 24 978.0 | (1.4) |
| *C. zealandicus* larvae | 5.4308 | (5.0) | 95 525.6 | (5.2) |
| *P. antipodarum* | 26.2407 | (24.3) | 128 123.0 | (7.0) |
| *G. maculatus* | 3.7755 | (3.5) | 83 491.4 | (4.5) |
| *R. retropinna* | 27.7230 | (25.7) | 575 889.9 | (31.4) |
| *C. carassius auratus* | 0.7469 | (0.7) | 15 636.3 | (0.9) |
| *G. cotidianus* | 37.8262 | (35.0) | 830 043.4 | (45.3) |
| Other | 1.9130 | (1.8) | 29 704.7 | (1.6) |
| | 107.9900 | | 1 831 884.4 | |

Table A.17. Estimated calorific values and dry weights of food species from stomachs of eels captured in winter. Percentage of total in brackets.

| Prey organism | Dry weight (g) | | Calorific value (joules) | |
|---|---|---|---|---|
| Oligochaeta | 0.0600 | (1.0) | 1 256.10 | (1.0) |
| Polychaeta | 0.0235 | (0.4) | 491.97 | (0.4) |
| *T. chiltoni* | 0.0166 | (0.3) | 345.43 | (0.3) |
| *A. annectens* | 0.0453 | (0.7) | 622.19 | (0.5) |
| *C. zealandicus* larvae | 0.0166 | (0.3) | 288.90 | (0.2) |
| *P. antipodarum* | 0.0102 | (0.2) | 38.10 | (0.03) |
| *G. cotidianus* | 5.8730 | (96.0) | 127 104.75 | (97.0) |
| Other | 0.0505 | (0.8) | 870.90 | (0.7) |
| | 6.0957 | | 131 018.34 | |

Table A.18.

LIST OF MEAN SIZES BY AGE AND YEAR CLASS
ORDER IS NO. OF CASES, MEAN SIZE (mm)

| | 1 | | 2 | | 3 | | 4 | | 5 | | 6 | | 7 | | 8 | | 9 | | 10 | | 11 | | 12 | | 13 | | 14 | | 15 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1931 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1932 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1933 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1934 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1935 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1936 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1937 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1938 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1939 | 1 | 88 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1940 | 1 | 0 | 1 | 160 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1941 | 0 | 0 | 0 | 0 | 1 | 176 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1942 | 1 | 88 | 0 | 0 | 0 | 0 | 1 | 191 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1943 | 0 | 0 | 1 | 191 | 0 | 0 | 0 | 0 | 1 | 199 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1944 | 0 | 0 | 0 | 0 | 1 | 210 | 0 | 0 | 0 | 0 | 1 | 217 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1945 | 2 | 88 | 0 | 0 | 0 | 0 | 1 | 230 | 0 | 0 | 0 | 0 | 1 | 243 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1946 | 1 | 88 | 2 | 161 | 0 | 0 | 0 | 0 | 1 | 242 | 0 | 0 | 0 | 0 | 1 | 251 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1947 | 0 | 0 | 1 | 184 | 2 | 180 | 0 | 0 | 0 | 0 | 1 | 255 | 0 | 0 | 0 | 0 | 1 | 256 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1948 | 4 | 88 | 0 | 0 | 1 | 210 | 2 | 199 | 0 | 0 | 0 | 0 | 1 | 268 | 0 | 0 | 0 | 0 | 1 | 263 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1949 | 1 | 88 | 4 | 176 | 0 | 0 | 1 | 238 | 2 | 214 | 0 | 0 | 1 | 288 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 271 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1950 | 3 | 88 | 1 | 174 | 4 | 199 | 0 | 0 | 1 | 253 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 304 | 0 | 0 | 0 | 0 | 1 | 288 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1951 | 0 | 0 | 3 | 173 | 1 | 200 | 4 | 215 | 0 | 0 | 1 | 283 | 2 | 240 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 320 | 0 | 0 | 0 | 0 | 1 | 301 | 0 | 0 |
| 1952 | 2 | 88 | 0 | 0 | 3 | 187 | 1 | 216 | 4 | 228 | 0 | 0 | 1 | 297 | 2 | 264 | 0 | 0 | 0 | 0 | 1 | 337 | 0 | 0 | 1 | 316 | 0 | 0 | 0 | 0 |
| 1953 | 5 | 88 | 2 | 164 | 0 | 0 | 3 | 207 | 1 | 262 | 4 | 245 | 0 | 0 | 1 | 319 | 2 | 284 | 0 | 0 | 0 | 0 | 1 | 350 | 0 | 0 | 1 | 346 | 0 | 0 |
| 1954 | 4 | 83 | 5 | 186 | 2 | 188 | 0 | 0 | 3 | 223 | 1 | 272 | 4 | 266 | 0 | 0 | 1 | 343 | 2 | 308 | 0 | 0 | 0 | 0 | 1 | 360 | 0 | 0 | 0 | 0 |
| 1955 | 0 | 0 | 4 | 164 | 5 | 211 | 2 | 205 | 0 | 0 | 1 | 245 | 1 | 287 | 4 | 283 | 0 | 0 | 1 | 359 | 2 | 322 | 0 | 0 | 1 | 400 | 0 | 0 | 0 | 0 |
| 1956 | 2 | 88 | 0 | 0 | 4 | 185 | 5 | 237 | 2 | 228 | 0 | 0 | 3 | 262 | 1 | 300 | 4 | 295 | 0 | 0 | 1 | 372 | 2 | 334 | 0 | 0 | 1 | 418 | 0 | 0 |
| 1957 | 3 | 83 | 2 | 178 | 0 | 0 | 4 | 206 | 5 | 265 | 2 | 243 | 0 | 0 | 3 | 278 | 1 | 314 | 4 | 316 | 0 | 0 | 2 | 384 | 0 | 0 | 2 | 0 | 0 | 0 |
| 1958 | 4 | 88 | 3 | 187 | 2 | 220 | 0 | 0 | 4 | 222 | 5 | 285 | 2 | 266 | 0 | 0 | 3 | 298 | 1 | 327 | 0 | 0 | 4 | 330 | 0 | 0 | 2 | 367 | 0 | 0 |
| 1959 | 5 | 83 | 4 | 175 | 3 | 205 | 2 | 246 | 0 | 0 | 4 | 240 | 5 | 302 | 2 | 276 | 0 | 0 | 3 | 316 | 1 | 335 | 0 | 0 | 1 | 425 | 0 | 0 | 0 | 0 |
| 1960 | 18 | 88 | 5 | 170 | 4 | 205 | 3 | 230 | 2 | 259 | 0 | 0 | 4 | 259 | 5 | 320 | 2 | 289 | 0 | 0 | 3 | 337 | 1 | 382 | 0 | 0 | 1 | 443 | 0 | 0 |
| 1961 | 11 | 88 | 18 | 177 | 5 | 204 | 4 | 221 | 3 | 253 | 2 | 288 | 0 | 0 | 4 | 297 | 5 | 336 | 2 | 309 | 0 | 0 | 3 | 379 | 1 | 379 | 0 | 0 | 0 | 0 |
| 1962 | 19 | 84 | 11 | 173 | 18 | 198 | 5 | 231 | 4 | 241 | 3 | 275 | 2 | 312 | 0 | 0 | 4 | 292 | 5 | 353 | 2 | 321 | 1 | 376 | 0 | 0 | 1 | 371 | 0 | 0 |
| 1963 | 10 | 83 | 19 | 177 | 11 | 197 | 18 | 220 | 5 | 259 | 4 | 261 | 3 | 299 | 2 | 329 | 0 | 0 | 4 | 302 | 5 | 367 | 2 | 391 | 1 | 391 | 0 | 0 | 1 | 393 |
| 1964 | 8 | 83 | 10 | 169 | 19 | 200 | 11 | 221 | 18 | 244 | 5 | 285 | 4 | 282 | 3 | 320 | 2 | 352 | 0 | 0 | 4 | 315 | 5 | 384 | 2 | 383 | 1 | 406 | 0 | 0 |
| 1965 | 5 | 88 | 8 | 185 | 10 | 192 | 19 | 221 | 11 | 246 | 18 | 264 | 5 | 306 | 4 | 297 | 3 | 335 | 2 | 363 | 0 | 0 | 4 | 332 | 1 | 363 | 0 | 0 | 0 | 0 |
| 1966 | 7 | 88 | 5 | 196 | 8 | 214 | 10 | 215 | 19 | 242 | 11 | 266 | 18 | 284 | 5 | 330 | 4 | 319 | 3 | 349 | 0 | 0 | 4 | 0 | 1 | 423 | 0 | 0 | 0 | 0 |
| 1967 | 4 | 88 | 7 | 166 | 5 | 222 | 8 | 236 | 10 | 241 | 19 | 263 | 11 | 282 | 18 | 303 | 5 | 347 | 4 | 331 | 0 | 0 | 4 | 404 | 2 | 366 | 0 | 0 | 0 | 0 |
| 1968 | 3 | 83 | 4 | 164 | 7 | 187 | 5 | 246 | 8 | 258 | 10 | 263 | 19 | 281 | 11 | 299 | 18 | 320 | 5 | 364 | 4 | 345 | 0 | 0 | 2 | 427 | 0 | 0 | 0 | 0 |
| 1969 | 1 | 88 | 3 | 174 | 4 | 193 | 7 | 208 | 5 | 268 | 8 | 278 | 10 | 285 | 19 | 299 | 11 | 316 | 18 | 338 | 4 | 379 | 2 | 360 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1970 | 0 | 0 | 1 | 199 | 3 | 200 | 4 | 206 | 7 | 228 | 5 | 294 | 8 | 299 | 10 | 310 | 19 | 320 | 11 | 335 | 18 | 358 | 4 | 393 | 2 | 378 | 0 | 0 | 0 | 0 |
| 1971 | 3 | 88 | 0 | 0 | 1 | 246 | 3 | 222 | 4 | 219 | 7 | 247 | 8 | 317 | 0 | 322 | 10 | 329 | 19 | 340 | 11 | 353 | 18 | 375 | 4 | 411 | 0 | 0 | 0 | 0 |
| 1972 | 3 | 88 | 3 | 158 | 0 | 0 | 1 | 289 | 3 | 243 | 4 | 237 | 7 | 268 | 8 | 337 | 0 | 0 | 10 | 348 | 19 | 359 | 11 | 369 | 18 | 391 | 0 | 0 | 0 | 0 |
| 1973 | 0 | 0 | 3 | 165 | 3 | 186 | 0 | 0 | 1 | 303 | 3 | 265 | 4 | 263 | 7 | 289 | 8 | 347 | 0 | 0 | 10 | 367 | 19 | 378 | 11 | 382 | 18 | 404 | 0 | 0 |
| 1974 | 0 | 0 | 0 | 0 | 3 | 199 | 3 | 222 | 0 | 0 | 1 | 319 | 3 | 285 | 4 | 284 | 7 | 313 | 0 | 0 | 0 | 0 | 19 | 0 | 11 | 396 | 18 | 397 | 0 | 0 |
| 1975 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 248 | 0 | 0 | 0 | 0 | 3 | 344 | 4 | 299 | 7 | 309 | 0 | 0 | 0 | 0 | 0 | 0 | 18 | 0 | 11 | 413 | 0 | 0 |
| 1976 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 251 | 0 | 0 | 0 | 0 | 3 | 359 | 4 | 362 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 18 | 416 | 0 | 0 |
| 1977 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Table A.18 continued

| | 16 | | 17 | | 18 | | 19 | | 20 | | 21 | | 22 | | 23 | | 24 | | 25 | | 26 | | 27 | | 28 | | 29 | | 30 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1931 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1932 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1933 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1934 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1935 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1936 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1937 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1938 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1939 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1940 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1941 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1942 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1943 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1944 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1945 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1946 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1947 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1948 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1949 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1950 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1951 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1952 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1953 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1954 | 1 | 355 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1955 | 0 | 0 | 1 | 364 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1956 | 0 | 0 | 0 | 0 | 1 | 381 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1957 | 1 | 428 | 0 | 0 | 0 | 0 | 1 | 390 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1958 | 0 | 0 | 1 | 442 | 0 | 0 | 0 | 0 | 1 | 403 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1959 | 0 | 0 | 0 | 0 | 1 | 455 | 0 | 0 | 0 | 0 | 1 | 417 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1960 | 2 | 393 | 0 | 0 | 0 | 0 | 1 | 471 | 0 | 0 | 0 | 0 | 1 | 426 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1961 | 1 | 461 | 2 | 410 | 0 | 0 | 0 | 0 | 1 | 489 | 0 | 0 | 0 | 0 | 1 | 437 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1962 | 0 | 0 | 1 | 479 | 2 | 422 | 0 | 0 | 0 | 0 | 1 | 503 | 0 | 0 | 0 | 0 | 1 | 444 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1963 | 4 | 406 | 0 | 0 | 1 | 500 | 2 | 442 | 0 | 0 | 0 | 0 | 1 | 513 | 0 | 0 | 0 | 0 | 1 | 453 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1964 | 1 | 391 | 4 | 428 | 0 | 0 | 1 | 512 | 2 | 459 | 0 | 0 | 0 | 0 | 1 | 523 | 0 | 0 | 0 | 0 | 1 | 464 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1965 | 3 | 423 | 1 | 402 | 4 | 443 | 0 | 0 | 1 | 530 | 2 | 470 | 0 | 0 | 0 | 0 | 1 | 529 | 0 | 0 | 0 | 0 | 1 | 475 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1966 | 0 | 0 | 3 | 439 | 1 | 414 | 4 | 459 | 0 | 0 | 1 | 545 | 2 | 482 | 0 | 0 | 0 | 0 | 1 | 536 | 0 | 0 | 0 | 0 | 1 | 483 | 0 | 0 | 0 | 0 |
| 1967 | 2 | 388 | 0 | 0 | 3 | 454 | 1 | 425 | 4 | 473 | 0 | 0 | 1 | 554 | 2 | 497 | 0 | 0 | 0 | 0 | 1 | 549 | 0 | 0 | 0 | 0 | 1 | 489 | 0 | 0 |
| 1968 | 5 | 445 | 2 | 402 | 0 | 0 | 3 | 467 | 1 | 434 | 4 | 488 | 0 | 0 | 1 | 572 | 2 | 508 | 0 | 0 | 0 | 0 | 1 | 556 | 0 | 0 | 1 | 498 | 0 | 0 |
| 1969 | 4 | 393 | 5 | 459 | 2 | 418 | 0 | 0 | 3 | 482 | 1 | 442 | 4 | 497 | 0 | 0 | 1 | 590 | 2 | 516 | 0 | 0 | 0 | 0 | 1 | 571 | 0 | 0 | 0 | 0 |
| 1970 | 0 | 0 | 4 | 415 | 5 | 472 | 2 | 435 | 0 | 0 | 3 | 498 | 1 | 448 | 4 | 512 | 0 | 0 | 1 | 605 | 2 | 528 | 0 | 0 | 0 | 0 | 1 | 586 | 0 | 0 |
| 1971 | 2 | 482 | 0 | 0 | 4 | 431 | 5 | 486 | 2 | 449 | 0 | 0 | 3 | 510 | 1 | 455 | 4 | 525 | 0 | 0 | 1 | 620 | 2 | 538 | 0 | 0 | 1 | 594 | 0 | 0 |
| 1972 | 3 | 437 | 2 | 497 | 0 | 0 | 4 | 443 | 5 | 497 | 2 | 476 | 0 | 0 | 3 | 525 | 1 | 465 | 4 | 534 | 0 | 0 | 1 | 626 | 2 | 546 | 0 | 0 | 0 | 0 |
| 1973 | 4 | 419 | 3 | 455 | 2 | 509 | 0 | 0 | 4 | 456 | 5 | 508 | 2 | 487 | 0 | 0 | 3 | 538 | 1 | 478 | 4 | 545 | 0 | 0 | 1 | 644 | 0 | 0 | 0 | 0 |
| 1974 | 5 | 466 | 4 | 432 | 3 | 469 | 2 | 520 | 0 | 0 | 4 | 467 | 5 | 522 | 2 | 507 | 0 | 0 | 3 | 548 | 1 | 489 | 4 | 555 | 0 | 0 | 2 | 557 | 0 | 0 |
| 1975 | 17 | 429 | 5 | 483 | 4 | 445 | 3 | 484 | 2 | 534 | 0 | 0 | 3 | 509 | 3 | 561 | 2 | 522 | 0 | 0 | 3 | 560 | 4 | 565 | 0 | 0 | 1 | 653 | 2 | 567 |
| 1976 | 2 | 429 | 5 | 419 | 0 | 0 | 2 | 420 | 1 | 530 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 580 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 675 |
| 1977 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

FREQUENCY DISTRIBUTION PLOT

Table A.19. Back calculated lengths for all eels (column three). Columns two and four represent lower and upper 95% confidence limits.

| Age class (mm) (1) | Lower limit (cm) (2) | Back calculated length (cm) (3) | Upper limit (cm) (4) | No. of cases (5) |
|---|---|---|---|---|
| 0 | 8.81 | 8.82 | 8.82 | 262 |
| 1 | 17.60 | 17.65 | 17.71 | 262 |
| 2 | 20.06 | 20.12 | 20.18 | 262 |
| 3 | 22.24 | 22.31 | 22.38 | 262 |
| 4 | 24.38 | 24.45 | 24.52 | 260 |
| 5 | 26.49 | 26.57 | 26.64 | 253 |
| 6 | 28.52 | 28.60 | 28.68 | 251 |
| 7 | 30.34 | 30.42 | 30.50 | 248 |
| 8 | 32.17 | 32.25 | 32.34 | 240 |
| 9 | 33.96 | 34.05 | 34.14 | 228 |
| 10 | 35.56 | 35.66 | 35.75 | 216 |
| 11 | 37.06 | 37.16 | 37.25 | 199 |
| 12 | 38.36 | 38.46 | 38.56 | 180 |
| 13 | 39.52 | 39.63 | 39.74 | 156 |
| 14 | 41.00 | 41.12 | 41.24 | 129 |
| 15 | 42.21 | 42.35 | 42.48 | 106 |
| 16 | 43.64 | 43.79 | 43.94 | 82 |
| 17 | 44.63 | 44.80 | 44.96 | 60 |
| 18 | 46.00 | 46.18 | 46.35 | 55 |
| 19 | 47.28 | 47.47 | 47.67 | 46 |
| 20 | 48.32 | 48.52 | 48.72 | 41 |
| 21 | 50.04 | 50.26 | 50.48 | 33 |
| 22 | 50.86 | 51.12 | 51.38 | 23 |
| 23 | 51.38 | 51.67 | 51.96 | 19 |
| 24 | 52.64 | 52.94 | 53.24 | 18 |
| 25 | 53.73 | 54.06 | 54.39 | 15 |
| 26 | 54.71 | 55.10 | 55.48 | 10 |
| 27 | 55.71 | 56.11 | 56.50 | 10 |
| 28 | 56.38 | 56.94 | 57.50 | 6 |

Table A.19 continued

Table A.19 continued

| | | | | |
|---|---|---|---|---|
| 29 | 57.47 | 58.05 | 58.63 | 6 |
| 30 | 55.06 | 55.76 | 56.46 | 3 |
| 31 | 55.25 | 56.21 | 57.17 | 2 |
| 32 | 55.79 | 56.76 | 57.73 | 2 |
| 33 | 56.30 | 57.26 | 58.21 | 2 |
| 34 | 52.97 | 52.97 | 52.97 | 1 |
| 35 | 53.64 | 53.64 | 53.64 | 1 |
| 36 | 54.10 | 54.10 | 54.10 | 1 |

Table A.20. Back calculated lengths for female eels (column three). Columns two and four represent lower and upper 95% confidence limits.

| Age class (mm) (1) | Lower limit (cm) (2) | Back calculated length (cm) (3) | Upper limit (cm) (4) | No. of cases (5) |
|---|---|---|---|---|
| 0 | 8.81 | 9.92 | 8.82 | 89 |
| 1 | 18.34 | 18.44 | 18.54 | 89 |
| 2 | 20.84 | 20.95 | 21.05 | 89 |
| 3 | 23.14 | 23.26 | 23.37 | 89 |
| 4 | 25.41 | 25.54 | 25.67 | 89 |
| 5 | 27.84 | 27.98 | 28.11 | 88 |
| 6 | 29.97 | 30.11 | 30.25 | 88 |
| 7 | 31.69 | 31.83 | 31.98 | 87 |
| 8 | 33.63 | 33.78 | 33.93 | 86 |
| 9 | 35.52 | 35.68 | 35.84 | 83 |
| 10 | 37.19 | 37.35 | 37.51 | 80 |
| 11 | 38.43 | 38.59 | 38.75 | 75 |
| 12 | 39.74 | 39.90 | 40.06 | 71 |
| 13 | 41.34 | 41.51 | 41.68 | 65 |
| 14 | 42.70 | 42.88 | 43.05 | 58 |
| 15 | 43.76 | 43.94 | 44.12 | 51 |
| 16 | 44.98 | 45.18 | 45.37 | 46 |
| 17 | 45.87 | 46.08 | 46.29 | 38 |
| 18 | 47.20 | 47.41 | 47.63 | 37 |
| 19 | 48.52 | 48.74 | 48.96 | 34 |
| 20 | 49.55 | 49.77 | 49.99 | 31 |
| 21 | 51.06 | 51.30 | 51.55 | 26 |
| 22 | 51.60 | 51.88 | 52.16 | 19 |
| 23 | 51.99 | 52.30 | 52.62 | 16 |
| 24 | 53.04 | 53.36 | 53.68 | 16 |
| 25 | 54.21 | 54.56 | 54.91 | 13 |
| 26 | 54.71 | 55.10 | 55.48 | 10 |
| 27 | 55.71 | 56.11 | 56.50 | 10 |
| 28 | 56.38 | 56.94 | 57.50 | 6 |

Table A.20 continued

Table A.20 continued

| | | | | |
|---|---|---|---|---|
| 29 | 57.47 | 58.05 | 58.63 | 6 |
| 30 | 55.06 | 55.76 | 56.46 | 3 |
| 31 | 55.25 | 56.21 | 57.17 | 2 |
| 32 | 55.79 | 56.76 | 57.73 | 2 |
| 33 | 56.30 | 57.26 | 58.21 | 2 |
| 34 | 52.97 | 52.97 | 52.97 | 1 |
| 35 | 53.64 | 53.64 | 53.64 | 1 |
| 36 | 54.10 | 54.10 | 54.10 | 1 |

Table A.21. Back calculated lengths for undifferentiated eels (column three). Columns two and four represent lower and upper 95% confidence limits.

| Age class (mm) (1) | Lower limit (cm) (2) | Back calculated length (cm) (3) | Upper limit (cm) (4) | No. of cases (5) |
|---|---|---|---|---|
| 0 | 8.81 | 8.82 | 8.82 | 173 |
| 1 | 17.18 | 17.25 | 17.31 | 173 |
| 2 | 19.62 | 19.70 | 19.77 | 173 |
| 3 | 21.75 | 21.82 | 21.90 | 173 |
| 4 | 23.80 | 23.88 | 23.96 | 171 |
| 5 | 25.73 | 25.81 | 25.90 | 165 |
| 6 | 27.69 | 27.78 | 27.87 | 163 |
| 7 | 29.56 | 29.66 | 29.75 | 161 |
| 8 | 31.30 | 31.40 | 31.50 | 154 |
| 9 | 33.02 | 33.12 | 33.23 | 145 |
| 10 | 34.55 | 34.66 | 34.77 | 136 |
| 11 | 36.17 | 36.29 | 36.41 | 124 |
| 12 | 37.40 | 37.52 | 37.65 | 109 |
| 13 | 38.16 | 38.30 | 38.44 | 91 |
| 14 | 39.53 | 39.69 | 39.85 | 71 |
| 15 | 40.69 | 40.87 | 41.05 | 55 |
| 16 | 41.80 | 42.02 | 42.25 | 36 |
| 17 | 42.34 | 42.58 | 42.82 | 22 |
| 18 | 43.39 | 43.64 | 43.89 | 18 |
| 19 | 43.58 | 43.87 | 44.16 | 12 |
| 20 | 44.32 | 44.65 | 44.97 | 10 |
| 21 | 46.07 | 46.39 | 46.71 | 7 |
| 22 | 47.13 | 47.50 | 47.88 | 4 |
| 23 | 47.85 | 48.29 | 48.73 | 3 |
| 24 | 48.98 | 49.56 | 50.13 | 2 |
| 25 | 50.19 | 50.80 | 51.40 | 2 |

Table A.22. Back calculated lengths for eels with otoliths of readability index two (column three). Columns two and four represent lower and upper 95% confidence limits.

| Age class (mm) (1) | Lower limit (cm) (2) | Back calculated length (cm) (3) | Upper limit (cm) (4) | No. of cases (5) |
|---|---|---|---|---|
| 0 | 8.81 | 8.82 | 8.82 | 170 |
| 1 | 17.55 | 17.62 | 17.69 | 170 |
| 2 | 20.14 | 20.22 | 20.30 | 170 |
| 3 | 22.33 | 22.41 | 22.50 | 170 |
| 4 | 24.56 | 24.65 | 24.74 | 169 |
| 5 | 26.73 | 26.83 | 26.93 | 162 |
| 6 | 28.64 | 28.74 | 28.85 | 159 |
| 7 | 30.38 | 30.49 | 30.59 | 155 |
| 8 | 32.08 | 32.20 | 32.31 | 148 |
| 9 | 33.44 | 33.56 | 33.67 | 135 |
| 10 | 34.91 | 35.04 | 35.16 | 125 |
| 11 | 36.54 | 36.67 | 36.81 | 114 |
| 12 | 37.77 | 37.91 | 38.05 | 101 |
| 13 | 38.74 | 38.90 | 39.05 | 75 |
| 14 | 40.39 | 40.56 | 40.74 | 64 |
| 15 | 41.72 | 41.91 | 42.10 | 55 |
| 16 | 42.74 | 42.97 | 43.21 | 37 |
| 17 | 43.85 | 44.10 | 44.36 | 27 |
| 18 | 45.30 | 45.58 | 45.86 | 23 |
| 19 | 46.36 | 46.66 | 46.97 | 20 |
| 20 | 47.60 | 47.94 | 48.29 | 16 |
| 21 | 50.82 | 51.16 | 51.49 | 13 |
| 22 | 51.27 | 51.67 | 52.08 | 9 |
| 23 | 52.17 | 52.62 | 53.06 | 7 |
| 24 | 54.15 | 54.62 | 55.08 | 6 |
| 25 | 54.34 | 54.87 | 55.40 | 5 |
| 26 | 56.25 | 56.97 | 57.69 | 3 |
| 27 | 57.58 | 58.33 | 59.07 | 3 |
| 28 | 65.39 | 65.39 | 65.39 | 1 |
| 29 | 67.50 | 67.50 | 67.50 | 1 |

Table A.23. Back calculated lengths for eels with otoliths of readability index three (column three). Columns two and four represent lower and upper 95% confidence limits.

| Age class (mm) (1) | Lower limit (cm) (2) | Back calculated length (cm) (3) | Upper limit (cm) (4) | No. of cases (5) |
|---|---|---|---|---|
| 0 | 8.81 | 8.82 | 8.82 | 193 |
| 1 | 17.44 | 17.50 | 17.56 | 193 |
| 2 | 19.82 | 19.89 | 19.96 | 193 |
| 3 | 21.93 | 22.01 | 22.08 | 193 |
| 4 | 23.93 | 24.01 | 24.09 | 190 |
| 5 | 25.99 | 26.07 | 26.16 | 185 |
| 6 | 27.95 | 28.04 | 28.13 | 182 |
| 7 | 29.84 | 29.93 | 30.03 | 179 |
| 8 | 31.67 | 31.76 | 31.86 | 175 |
| 9 | 33.46 | 33.56 | 33.67 | 168 |
| 10 | 35.15 | 35.26 | 35.36 | 158 |
| 11 | 36.42 | 36.53 | 36.64 | 145 |
| 12 | 37.65 | 37.77 | 37.88 | 128 |
| 13 | 39.08 | 39.20 | 39.33 | 114 |
| 14 | 40.67 | 40.81 | 40.96 | 95 |
| 15 | 41.68 | 41.84 | 42.00 | 74 |
| 16 | 42.83 | 43.01 | 43.19 | 55 |
| 17 | 43.97 | 44.18 | 44.38 | 41 |
| 18 | 45.28 | 45.49 | 45.70 | 40 |
| 19 | 46.51 | 46.74 | 46.98 | 32 |
| 20 | 47.95 | 48.20 | 48.44 | 29 |
| 21 | 48.78 | 49.05 | 49.32 | 24 |
| 22 | 48.82 | 49.11 | 49.41 | 17 |
| 23 | 49.81 | 50.13 | 50.46 | 14 |
| 24 | 50.39 | 50.73 | 51.06 | 12 |
| 25 | 52.28 | 52.66 | 53.03 | 9 |
| 26 | 53.68 | 54.18 | 54.67 | 6 |
| 27 | 54.65 | 55.14 | 55.64 | 6 |

Table A.23 continued

Table A.23 continued

| | | | | |
|---|---|---|---|---|
| 28 | 54.64 | 55.15 | 55.68 | 5 |
| 29 | 55.73 | 56.30 | 56.91 | 4 |
| 30 | 54.44 | 55.39 | 56.34 | 2 |
| 31 | 55.25 | 56.21 | 57.17 | 2 |
| 32 | 55.79 | 56.76 | 57.73 | 2 |
| 33 | 56.30 | 57.26 | 58.21 | 2 |
| 34 | 52.97 | 52.97 | 52.97 | 1 |
| 35 | 53.64 | 53.64 | 53.64 | 1 |
| 36 | 54.10 | 54.10 | 54.10 | 1 |

Table A.24. Back calculated lengths for eels with otoliths of readability index four (column three). Columns two and four represent lower and upper 95% confidence limits.

| Age class (mm) (1) | Lower limit (cm) (2) | Back calculated length (cm) (3) | Upper limit (cm) (4) | No. of cases (5) |
|---|---|---|---|---|
| 0 | 8.81 | 8.82 | 8.82 | 62 |
| 1 | 17.72 | 17.84 | 17.96 | 62 |
| 2 | 20.14 | 20.28 | 20.42 | 62 |
| 3 | 22.41 | 22.57 | 22.72 | 62 |
| 4 | 24.48 | 24.65 | 24.81 | 61 |
| 5 | 26.55 | 26.73 | 26.90 | 60 |
| 6 | 28.57 | 28.75 | 28.94 | 60 |
| 7 | 30.35 | 30.54 | 30.73 | 60 |
| 8 | 32.41 | 32.61 | 32.81 | 59 |
| 9 | 34.26 | 34.47 | 34.69 | 57 |
| 10 | 35.19 | 35.40 | 35.61 | 50 |
| 11 | 36.95 | 37.18 | 37.41 | 44 |
| 12 | 38.40 | 38.64 | 38.89 | 42 |
| 13 | 39.68 | 39.96 | 40.25 | 34 |
| 14 | 40.20 | 40.51 | 40.81 | 27 |
| 15 | 41.82 | 42.14 | 42.46 | 25 |
| 16 | 43.56 | 43.91 | 44.25 | 23 |
| 17 | 44.62 | 44.98 | 45.33 | 19 |
| 18 | 46.36 | 46.74 | 47.11 | 17 |
| 19 | 47.19 | 47.60 | 48.01 | 15 |
| 20 | 46.62 | 47.04 | 47.46 | 11 |
| 21 | 50.11 | 50.54 | 50.96 | 7 |
| 22 | 51.80 | 52.28 | 52.75 | 6 |
| 23 | 52.51 | 52.95 | 53.49 | 5 |
| 24 | 53.32 | 53.87 | 54.42 | 5 |
| 25 | 54.48 | 55.12 | 55.76 | 4 |
| 26 | 53.50 | 53.68 | 53.86 | 2 |
| 27 | 54.11 | 54.30 | 54.50 | 2 |
| 28 | 55.01 | 55.01 | 55.01 | 1 |
| 29 | 55.60 | 55.60 | 55.60 | 1 |
| 30 | 56.50 | 56.50 | 56.50 | 1 |

# Study of Ellesmere eel fishery

Parliamentary reporter

A working party has been set up by the Minister of Fisheries (Mr Bolger) to study the establishment of a controlled fishery for eels in Lake Ellesmere.

The Ellesmere eels were being over-exploited, he said, and unless a limit was placed on the number of fishermen there was a very real possibility of serious long-term depletion of stocks.

There would be a stay of new licences.

In 1976, eels had ranked as New Zealand's third most important export fish after rock lobster (crayfish), and snapper, said Mr Bolger. Nearly 1700 tonnes of eel, worth about $2.2M, had been exported that year and nearly a third of these had been caught in Lake Ellesmere.

Eel landing from the lake had increased from 5 tonnes in 1966-67 to 647 tonnes in 1975-76, before dropping back to 560 tonnes in 1976-77, in spite of a 45 per cent increase in fishing effort.

The latest figures represented a yield of more than 30kg per hectare of lake area, considerably higher than for established European eel fisheries, where the growth rate was faster and the lake were stocked artificially with elver, said Mr Bolger.

This strongly suggested that the fishery was being overworked and that conservation measures were necessary, he said.

Fig. 14. Newspaper clipping. Christchurch Press, 8.3.1978.

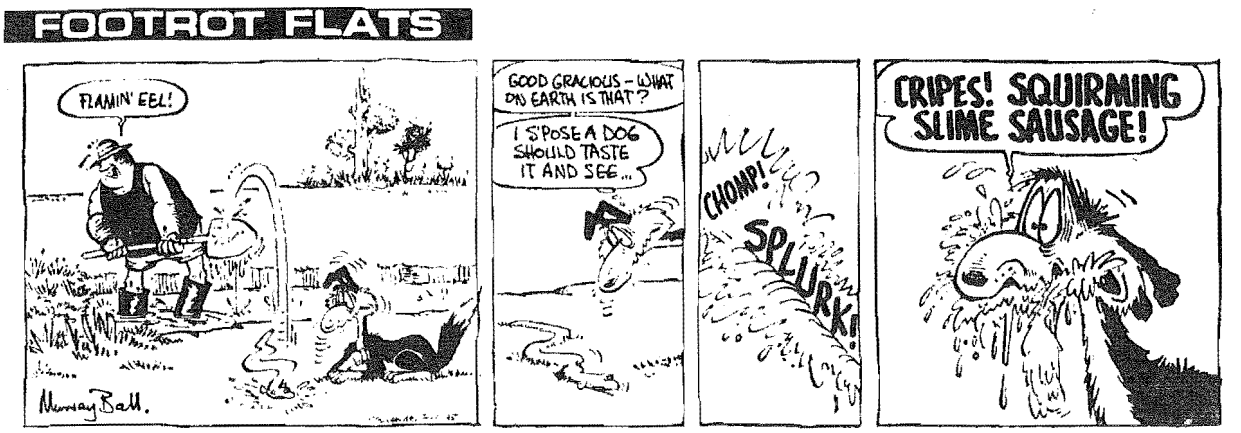


Fig. 15. Endpiece. Wal Cadwallader's "dog" has the final word.